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Fire Regime Dynamics Following the Mid-Holocene Hemlock Decline in Eastern North America

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FIRE REGIME DYNAMICS FOLLOWING THE MID-HOLOCENE HEMLOCK DECLINE IN EASTERN NORTH AMERICA

A Dissertation Presented

by

KENNEDY H. CLARK

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Forest Resources Graduate Program

FIRE REGIME DYNAMICS FOLLOWING THE MID-HOLOCENE HEMLOCK DECLINE IN EASTERN NORTH AMERICA

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DEDICATION

Dedicated to
Persephone and Atticus

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ABSTRACT

FIRE REGIME DYNAMICS FOLLOWING THE MID-HOLOCENE HEMLOCK DECLINE IN EASTERN NORTH AMERICA

MAY 2010

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Approximately 5,000 years ago, eastern hemlock (*Tsuga canadensis*) experienced a sudden, rapid, range-wide decline most probably due to pest, disease, or climate change. An aphid-like defoliating insect, the hemlock woolly adelgid (*Adelges tsugae*), recently (1950's) introduced to eastern North America has been spreading across the eastern United States. The adelgid attacks all size and age classes of hemlocks causing up to 95% mortality in affected stands. The potential for another range-wide hemlock decline has raised a number of concerns including the increased threat of wildfire.

Altered fuel loadings in modern adelgid-affected stands and the effects of presumably similar changes in fuels and subsequently altered fire regimes following the prehistoric decline are examined. Fuels data from an adelgid-infested stand in Connecticut and an uninfested stand in Massachusetts were used to generate custom fuel models and predict fire behavior in each stand. Sediment cores were extracted from three sites in western Massachusetts and analyzed for fossil pollen and charcoal around the period of the prehistoric decline. Fossil data from two previously studied sediment cores from coastal Maine are included in the analysis.

Results demonstrate a clear and highly significant increase in both fuel loadings and predicted fire behavior in the modern, adelgid-affected stand. Three of the coring sites reflect distinct, significant, short-lived increases in charcoal associated with the prehistoric decline; two do not. Results from the first three sites suggesting increased fire activity also were associated with changes in vegetation which indicate disturbance. Increased fire activity after the decline seems most pronounced in areas where fire was common before the decline. Results indicate that fire was not universally a significant factor driving post-decline succession. Research across a broader geographic area is needed to clarify the relationship between fire and hemlock following the mid-Holocene decline, but the results presented here suggest that managers of modern stands affected by the adelgid should include the possibility of intense fires as a threat to landscapes heavily affected by hemlock decline.

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CHAPTER 1

INTRODUCTION

Context

Basic Ecology of Hemlock

Eastern hemlock (*Tsuga canadensis* L.) is a long-lived, shade-tolerant, disturbance-intolerant conifer (Baker 1949, Tubbs 1977). Individuals may reach ages of 800 years (although that is uncommon), and may take as much as 250 to 300 years to reach maturity, but sexual reproduction may begin as early as age 15 (Godman and Lancaster 1990). The species grows in cool, humid sites in acidic, moist, but well-drained soils at elevations ranging from sea-level to over 1,500 meters (Fuller 1998, Godman and Lancaster 1990). Hemlock is an important component species of many forests of northeastern North American, and because of its longevity and sensitivity to disturbance, hemlock is frequently dominant or co-dominant in old growth stands (Foster and Zebryk 1993). D'Amato and Orwig (2008) found in a study of the 18 largest remaining old-growth stands in Massachusetts that hemlock dominance by basal area ranged from 61% to 81%.

Rogers (1980) found that near its northern range limit hemlock is typically the dominant species only in relatively small stands (0.04 to 2.4 ha), while D'Amato and Orwig (2008) found hemlock to be dominant in many larger stands (5 to 13 ha). Modern hemlock achieves dominance most frequently where soils are shallow, low in nutrients, and moistened by micro-climate or seepage (Rogers 1978). On these sites, hemlock's primary competitors - shade-tolerant species such as sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and red spruce (*Picea rubens*) - cannot survive suppression (via shading and soil nutrient competition) by adult hemlocks. Hemlock also will grow on moist, deep, upland soils that are nutrient-rich, but does not dominate in these areas because of competition from mesic hardwoods, many of which respond to disturbance with vigorous sprouting (Rogers 1978). Before European settlement, hemlock was more widespread and co-dominant in many forests including those with rich soils.

D’Amato and Orwig (2008) report that, historically, hemlock-dominated old-growth stands in western Massachusetts were characterized by relatively frequent, low intensity disturbance with no evidence of stand-replacing disturbances. In a study from 1962 to 1994, Woods (2000) found that in Michigan, hemlock was the ultimate competitive dominant at most sites, but requires a millennium or more without major disturbance to displace sugar maple and other competitors. Subsequent to European settlement, clearing for agriculture and exploitation of hemlock as a source of timber and tannins (from the bark) now restricts hemlock to thin-soiled or nutrient-poor sites where clearing was less common and competition from other shade-tolerant tree species less intense (Rogers 1978, McMartin 1992).

Both cones and seed on eastern hemlock are small for the genus: cones are from 13 to 19 mm in length; seeds average 1.6 mm in length not including a small terminal “wing” (Godman and Lancaster 1990). Because of the small size of the wing, hemlock seeds do not usually disperse farther than tree-height, but further distribution may occur from drifting over crusted snow (Godman and Lancaster 1990). Cone (and seed) production is normally high, but seed viability is low. Hemlock seeds germinate best on moist substrates, and grow especially well on rotten wood and moss beds, although these substrates may lead to weak root systems and increased windthrow (Godman and

Lancaster 1990). "Tip-up mounds" formed by root masses from fallen trees and decayed, moss-covered logs often serve as hemlock nurseries. Seedlings grow slowly, are highly shade-tolerant, and are very sensitive to drought (Godman and Lancaster 1990). Hemlock seedlings are able to establish under canopies of mature trees. Hemlocks do not reproduce vegetatively (Godman and Lancaster 1990).

Eastern hemlocks, especially seedlings and saplings, are very susceptible to fire because of their thin bark, often shallow roots, low-branching habits, and heavy litter deposits (FEIS 2002). Hemlock often escapes the influence of fire, because it grows in moist habitats or in association with non-fire-prone vegetation such as northern hardwoods. Even low-intensity fires will readily kill hemlock seedlings and saplings, and fires burning under drought conditions may kill adult trees (FEIS 2002).

In the past, hemlock wood has been used for light framing, sheathing, roofing, subflooring, boxes, and crates (Godman and Lancaster 1990). Hemlock bark was used extensively in the tanning industry, particularly in the 19th century in the Northeast (McMartin 1992). Currently, hemlock is used for pulp and in the ornamental, nursery, and horticultural market (Goldman and Lancaster 1990).

Yamasaki *et al.* (2000) found 96 bird and 47 mammal species are associated with the hemlock forests in the northeastern United States. Of these species, eight bird species (great horned owl, long-eared owl, northern saw-whet owl, solitary vireo, blue jay, red-breasted nuthatch, hermit thrush, and black-throated green warbler) and ten mammal species (snowshoe hare, red squirrel, deer mouse, southern red-backed vole, porcupine, red fox, black bear, marten, bobcat, and white-tailed deer) are strongly associated with the hemlock forests though none of these species are limited to it.

Past Distribution and Dynamics

After the Wisconsin glaciation, hemlock migration reached southern New England about 12,000 to 10,000 ^{14}C yrs BP (radiocarbon years before present); initially expanding along the Appalachian Mountain axis from southwest to northeast. Hemlock then spread north and west reaching Maine and Michigan approximately 8,000 ^{14}C yrs BP establishing the full extent of its maximum range (Davis 1981A, Gaudreau 1986, Williams *et al.* 2004). At that time, hemlock typically comprised as much as 40% of all fossil pollen. Paleoecological evidence indicates that hemlock rose to a greater level of abundance in northeastern North America from 8,000 to 5,000 ^{14}C yrs BP (corresponding with the mid-Holocene hypsothermal period) than at any other time in the last 10,000 years (Davis 1981B, Gaudreau 1986). At 4750 ^{14}C yrs BP or approximately 5,500 cal. yrs BP (calendar years before present), hemlock experienced a sudden, rapid, range-wide decline during which hemlock percentages fell to less than 10% in most sediments (Bennet and Fuller 2002, Davis 1981B, Williams *et al.* 2004). Despite low abundances, hemlock's distribution remained nearly unchanged, contracting only slightly at the southwest extent of its range (Williams *et al*. 2004). Hypotheses regarding the cause of the decline include a biotic agent - possibly a disease, an insect pest, or an insect-disease complex - (Davis 1981B, Patterson and Backman 1988, Fuller 1998) or climate change as the primary cause (Foster *et al.* 2006). In some areas, hemlock populations recovered to their previous levels within 1,000 to 2,000 years, but populations never reached pre-decline levels elsewhere (Fuller 1998). Currently, eastern hemlock occurs throughout the northeastern and north-central United States and adjacent Canada and into the higher elevations of the southern Appalachian region (Gleason and Cronquist 1991, Godman and Lancaster 1990).

Current Threats to Hemlock

Today, there are relatively few native pathogens and pests that attack hemlock. Seeds are sensitive to several molds and seedlings to several damping-off fungi and root rots (Godman and Lancaster 1990). On adult trees, several rusts may affect needles and twigs and a number of rots and fungi may affect the bole and roots. These pathogens may stress trees, lower their value as timber, or interrupt reproduction, but rarely do they cause tree death by themselves – especially across wide portions of forested landscapes (Godman and Lancaster 1990). There are approximately two dozen insects that will attack eastern hemlock, but of these only the hemlock borer (*Melanophila fulvoguttata*), spruce budworm (*Choristoneura fumiferana*), the hemlock looper (*Lambdina fiscellaria fiscellaria*), and the exotic hemlock woolly adelgid (*Adelges tsugae* Annand) cause significant damage (Godman and Lancaster 1990, Orwig and foster 1998). Elongate hemlock scale (*Fiorinia externa*) is also a threat to hemlock. While elongate hemlock scale does not usually cause mortality of trees, infestation by the scale makes individuals more susceptible to adelgid, borer, or root rot infestations (Penn State 2010).

An aphid-like defoliating insect, the hemlock woolly adelgid was introduced to eastern North America from Asia in the early 1950's (Souto *et al.* 1996). The adelgid attacks all size and age classes of hemlocks, which seem to have no natural resistance to the parasite (Orwig and Foster 1998). Up to 95% mortality has been observed in affected stands (Orwig and Foster 1998). Substantial range-wide reductions in populations of eastern hemlock can be expected if the adelgid continues to spread unimpeded through hemlock's current range (Orwig and Foster 1998).

The potential for another range-wide hemlock decline has raised many questions regarding the vegetation of northern forests. Albani and Moorcroft (2003) state that “[hemlock’s] loss and replacement by birch and other hardwoods will likely lead to a dramatic cascade of biological, biogeochemical, and physical changes.” Concerns include what species will replace hemlock and for how long (Dougherty 2001, Heard and Valente 2009), affected stands being invaded by non-native species (Evans 2002a), effects on forest streams (Colburn and Orwig 2003), changes in ant community structure (Ellison *et al.* 2005a), consequences for forest structure and dynamics (Ellison *et al.* 2005b), and economic impacts on residential landscape values (Holmes *et al.* 2005). Curiously, there is little study of the economic effects from loss of hemlock timber, probably because of the relatively low utilization and value of the species (Luppold and Sendak 2004, Godman and Lancaster 1990). Similarly, there is little concern about increased fuel loads in affected stands even though the potential for increased occurrence of wildfires has ecological and public safety implications. Although old growth stands may generate significant quantities of heavier fuels (dead wood) (Tyrrell and Crow 1994), hemlock forests are normally thought to be fire resistant due to moist soil conditions, heavy shading, and low surface fuel loadings (Foster and Zebryk 1993). I hypothesize, however, that adelgid-caused mortality could create large quantities of both heavy and fine fuels which could increase the likelihood of high-intensity fires in areas where such fires are not normally expected.

Fossil pollen and charcoal analyses of sediments associated with the mid-Holocene decline of eastern hemlock might provide insight on the effects of adelgid-mortality on fires in modern hemlock stands. Foster and Zebryk (1993) noted a charcoal horizon contemporaneous with the mid-Holocene decline in two sediment cores from western Massachusetts. They examined macroscopic charcoal layers in peat (which indicate fires burned at the core site), and hypothesized that a large fire burned through during or soon after the hemlock decline. Unpublished data by Natalie E. R. Drake from two sites on Mount Desert Island, Maine - Lake Wood and The Bowl - clearly show increased charcoal abundance coincident with the hemlock decline. Davis *et al.* (1985), however, note no change in charcoal abundance following the hemlock decline in sediments of Mirror Lake in New Hampshire’s White Mountains. No other studies have investigated the link between the prehistoric hemlock decline and increased fire incidence.

Analytical Framework

This work examines changes in fire regimes, if any, following the mid-Holocene hemlock decline. The questions addressed are: (1) Were there changes in fire regimes following the mid-Holocene hemlock decline? (2) If so, what sort of change occurred? (3) Is there evidence that the modern adelgid-caused decline might follow a similar pattern? To a lesser extent, questions regarding vegetation changes and tangential issues such as causes of the mid-Holocene decline will also be examined.

The analytical framework of this project is modeled after E. David Ford’s Scientific Method for Ecological Research (1976). Ford recognizes the difficulties of researching ecological systems stemming from their inherent complexity and variability.

He presents an extension to traditional scientific method based on a progressive synthesis of information along a path of "logic for discovery". The path consists primarily of defining what is known (or assumed to be known): What is the question?; What data are needed to answer the question?; and What can be inferred from the data? To this end, Ford recommends an analytical framework consisting of "three types of knowledge: axioms, what we assume we know; postulates, what questions we have but stated in a propositional form so they can be classified as true or false using the research; and data statements, which define the data needed to classify the postulates as true, false, or acceptable within a certain probability."

Axioms

Axioms are statements which are known or assumed to be true, based largely on previous research. There are four axioms related to this project.

First, eastern hemlock experienced a rapid, severe, range-wide decline at about 5,000 years B.P. This fact, as discussed above, is well-supported in the literature including Davis (1981B), Webb (1982), and Bennet and Fuller (2002).

Second, pollen and charcoal left in sediments of lake or wetlands provide evidence of the vegetation and fire history of an area. This is a generally true statement and the technical methodologies for fossil pollen and charcoal analysis are well-established (Faegri and Iverson 1975, Ogden 1977, Patterson *et al.* 1987, Clark 1988). There is, however, an underlying assumption of fossil pollen analysis that the percentages of pollen in sediments reflect the importance of species on the landscape at the time the sediment was deposited. This assumption is, in fact, flawed. Insect pollination, differential volumes of pollen produced by different species, mode of transport of pollen to sediments, and other factors prevent a direct correlation between pollen abundances and species abundances. This concept is examined in detail in Davis (1963) and Davis and Goodlett (1960). Charcoal analysis has a similar assumption and similar problems; in this case based largely on particle size, type of transport (in air or water), and distance from source (Patterson *et al.* 1987). It is up to the analysts' knowledge physical factors influencing the production, transportation and sedimentation of fossil material, and of the autecology and synecology of the various species involved to accommodate departures from the fundamental assumptions in the final analysis of the data.

The third axiom is that hemlock woolly adelgid is causing a decline of hemlock in modern stands similar to the mid-Holocene decline, at least at a local scale. This concept is also well-supported in the literature (*e.g.*, Orwig and Foster 1998).

Finally, large-scale mortality of vegetation contributes to greater amounts of available fuels. If fires occur, higher fuel loadings lead to larger, more intense, and more severe fires. Although these statements seem intuitively true (especially to those with experience controlling wildland fire), they are also well-supported by research data. The increased fuel loading/increased fire behavior link is perhaps best illustrated quantitatively in the fire behavior modeling system developed by Rothermel (1983) which continues to be used as a basis of fire behavior prediction. Additional support can be found in Anderson (1982), Amos (1941), and Jolley (2001).

Postulates

With axioms established, research questions (postulates) can be formulated and stated in propositional form. There are five postulates for this study:

1. Hemlock mortality produces heavy fuel loadings where loadings are normally low or moderate.
2. Frequent, high-intensity fires outside of the "normal" fire regime of low frequency/low intensity fires in hemlock stands occurred following the decline 5000 years ago.
3. Changes in the fire regime were short-lived, persisting only until the increased fuel-load was consumed or decomposed and hemlock was replaced with non-fire-prone species such as birch.
4. In New England, altered fire regimes were more likely to occur in areas where the existing fire frequency and intensity were higher and/or ignition sources (*i.e.*, people) more abundant.
5. Hemlock was quickly (within a decade or two) replaced by pioneering tree species such as birch, and stands succeeded to northern hardwoods, pine, or other mature hemlock competitors until hemlock recovered centuries later.

Data Statements

With the axioms and postulates established, information needed to answer the questions were defined. These data statements define what is needed to classify the postulates as true or untrue. First, fuel loading data from one healthy and one dead (but unsalvaged) modern hemlock stand were needed so that fire behavior estimates could be obtained. Fuel loading and predicted fire behavior data facilitated assessment of postulate one. The two stands were chosen so as to illustrate the extremes of mortality (*i.e.*, nearly all hemlock dead and nearly no hemlock dead) to demonstrate that postulate 1 is reasonable. The fuels assessment was not intended to examine the full range of variability in hemlock mortality affected fuel loads or fire behavior (more stands across a broader range of mortality levels would be needed to do so). Second, fossil pollen and charcoal analysis of sediment cores from several locations were needed. Cores from areas where fire is presumed to have been common and areas where it is presumed to have been uncommon before the decline were collected and analyzed. Sampling focused on the period just before, during, and just after the decline. These data facilitated assessment of postulates two through five.

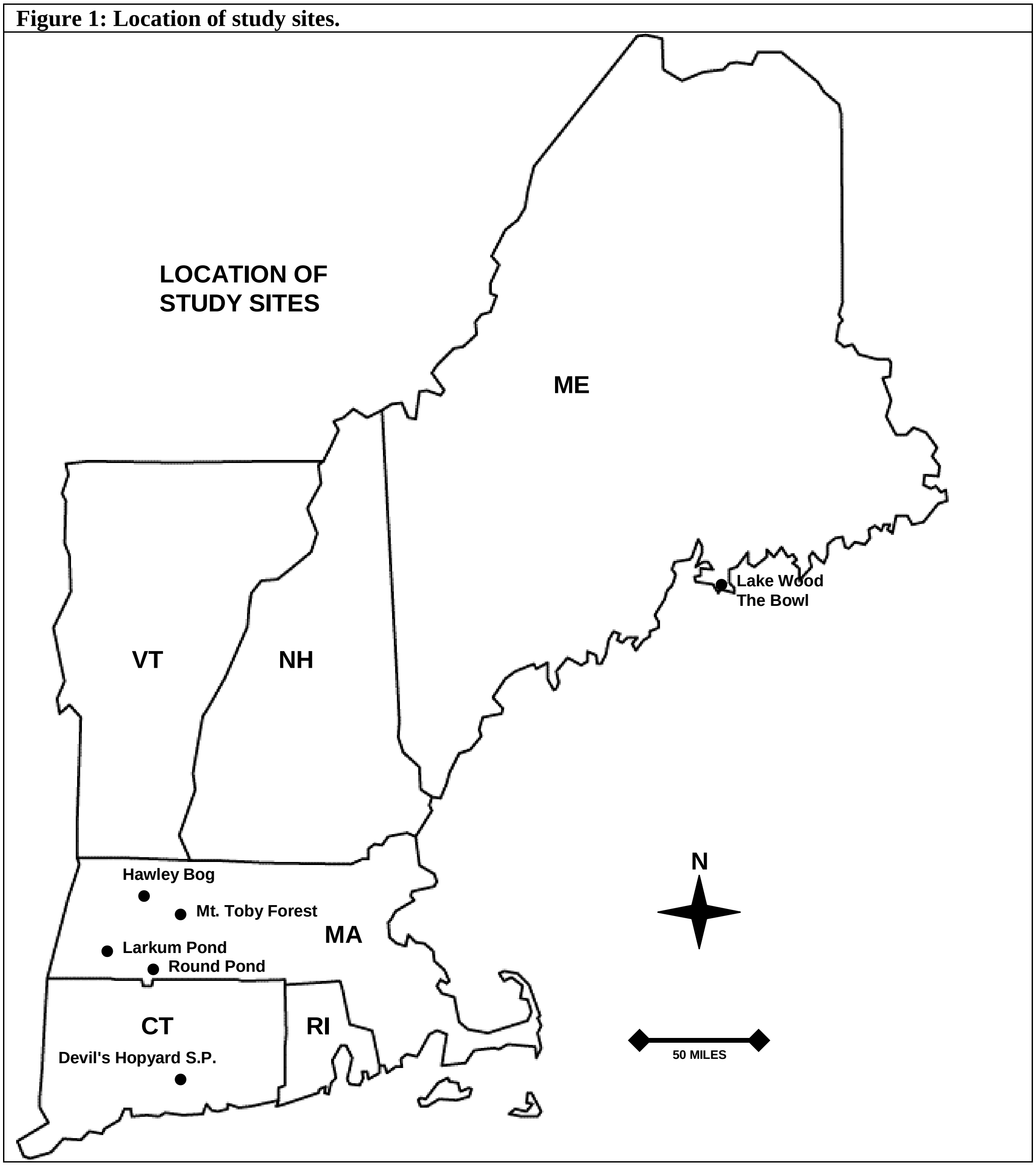
Study Sites

Seven sites were sampled for this project. Modern stands from two locations were used for the fuels analysis: Mount Toby Demonstration Forest in Sunderland, Massachusetts; and Devil's Hopyard State Park in East Haddam, Connecticut (Figure 1). Pollen and charcoal data were available from The Bowl and Lake Wood, two previously sampled sites on Mount Desert Island, Maine (Figure 1). Three sites in western Massachusetts were sampled for pollen and charcoal data: Hawley Bog in Hawley, Larkum Pond in Otis, and Round Pond in Westfield (Figure 1). These three sites represent a gradient from low fire incidence (Hawley Bog) to high fire incidence (Round Pond).

Mount Toby Demonstration Forest

Mount Toby Demonstration Forest is located in Sunderland, Massachusetts. The sampling area is a mature hemlock stand located on a north-facing slope of Ox Hill at approximately 42^{O} 29' 15" N, 72^{O} 32' 15" W. The sampling area lies at about 200 meters in elevation on a 10-40% slope. Soils are extremely rocky, fine sandy loams derived from glacial till. Vegetation is strongly dominated by mature hemlock with black birch (*Betula*

Figure 1: Location of study sites.



lenta), beech, and sugar maple (*Acer saccharum*) comprising a significant component of the canopy (Table 1). The understory is sparse with seedlings and saplings of the canopy species along with limited shrub and herb components. This site was chosen as being representative of a healthy hemlock stand unaffected by adelgid. Since the time of sampling, the stand has been significantly affected by ice and wind.

Table 1: Basal area by species for fuels study sites in m²/ha (ft²/ac).

species	**Mount Toby**	**Devil’s Hopyard**
hemlock (live)	29.2 (127)	0.5 (2)
hemlock (dead standing)	0.5 (2)	19.3 (84)
black birch	6.2 (27)	4.1 (18)
beech	2.8 (12)	1.4 (6)
sugar maple	2.5 (11)	0.9 (4)
white ash	0.9 (4)	0
northern red oak	0.5 (2)	1.8 (8)
pignut hickory	0	1.4 (6)
total (live)	**42.1 (183)**	**10.1 (44)**

Devil’s Hopyard State Park

The stand is located on an outparcel of Devil’s Hopyard State Park at 41^{O} 27” 30” N, 72^{O} 20’ 30” W in East Haddam, Connecticut (Figure 1). This site was chosen to represent a stand of hemlock with nearly 100% adelgid-caused mortality. Standing dead hemlock comprises 19.3 m²/ha (84 ft²/ac), while live hemlock is only 0.5 m²/ha (2 ft²/ac). Hemlock was likely more dominant than represented by the post-adelgid basal area figures as numerous dead trees had fallen at the time of sampling. Remnant overstory trees including black birch, northern red oak (*Quercus rubrum*), and beech are scattered within the stand (Table 1). Understory vegetation is dominated by black birch (*Betula lenta*) saplings. Soils are a complex of gravelly fine sandy loams derived from glacial till. This stand lies on fairly flat ground at about 150 m on the floodplain of a nearby creek (Eightmile River).

Hawley Bog

Hawley Bog, jointly owned by The Nature Conservancy and Five Colleges, Inc., lies at 42^{O} 34’ 30” N, 72^{O} 53’ 30” W in Hawley, Massachusetts (Figure 1). This site is a true bog at about 540 m in elevation on a flat plain. The bog is approximately 26 ha in size with around 2 ha of open water. Soils surrounding the peat and muck of the bog are very rocky fine sandy loams and very stony loams. Hawley Bog is a pond with no inlet and one outlet (Potash Brook). An unconsolidated peat mat has formed in most of the pond over millennia which now reaches a maximum depth of 8 to 9 meters. Limnic sediments underlie the peat mat and constitute the substrate of the center, open part of the pond. The peat mat supports typical northern bog herbaceous and shrub vegetation including many sedges, rushes, and several carnivorous plants. The surrounding forest is northern hardwoods with sugar maple, beech, birch, and hemlock comprising the dominant species. Hawley Bog was chosen as a coring site because of its presumably low prehistoric fire incidence. During the Holocene, it probably had a cooler, moister climate and lower populations of prehistoric peoples to act as ignition sources than the other sites. It has been fairly isolated from human disturbance since European settlement. The Town of Hawley is currently home to only 336 residents (US Census Bureau 2007).

Larkum Pond

Larkum Pond is located in Otis, Massachusetts, population 1,394 (US Census Bureau 2007) at 42^{O} 10’ 10” N , 73^{O} 04’ 30” W (Figure 1). This 10-ha pond lies at 380 m elevation in a deep kettle among hilly terrain with steep slopes surrounding the pond to the east, north, and west. Soils are fine sandy loams, sandy loams, and gravelly sandy loams derived from glacial till. The pond has no inlets and one outlet (an unnamed tributary of Fall River). Land slopes steeply 50 meters or more down to the pond surface from the surrounding hills. Larkum Pond is the only coring site which has surrounding vegetation currently strongly dominated by hemlock. White pine, birch, sugar maple, and beech are also abundant. The mid-Holocene fire regime at Larkum Pond is presumed to have been intermediate between Hawley Bog and Round Pond. The lower elevation (by 160 m) of Larkum Pond relative to Hawley Bog contributes to warmer drier climate. There are a number of other natural ponds in the vicinity of Larkum Pond that may have supported a larger aboriginal population than Hawley Bog.

Round Pond

Round Pond was chosen for its presumed high incidence of fire during the mid-Holocene. Round Pond is surrounded by droughty, loamy sand soils of a glacial outwash plain which support more drought-tolerant, fire-prone species like pitch pine (*Pinus rigida*) and scrub oak (*Quercus ilicifolia*). Due to its location in the Connecticut Valley, Round Pond likely had the highest population of indigenous people of the three western Massachusetts sites and was thus exposed to more ignition sources (Patterson and Sassaman 1988). A coastal site would have been ideal in terms of fire incidence, but hemlock has never been abundant along the coast of southern New England. Round Pond itself is a true ice block depression (kettle) pond with no inlet or outlet. It is part of a system of similar ponds in close proximity to one another in Hampton Ponds area of Westfield, MA (42^{O} 10’ 30” N, 72^{O} 42’ 20” W, Figure 1). Round Pond, about 2 ha in size, lies at 260 m in elevation with steep but low banks up to the surrounding plain. Between the open water and the slope of the pond shore is a narrow peat mat currently dominated by grasses, sedges, rushes, and buttonbush (*Cephalanthus occidentalis*). With over 40,000 residents in Westfield (US Census Bureau 2007), the area around Round Pond is much more densely populated than the areas around Hawley Bog or Larkum Pond with houses and a road occurring very close to the pond.

The Bowl and Lake Wood

Sediments from The Bowl and Lake Wood were analyzed in 1990 by Natalie E. R. Drake. Although never published, the data were used in this project to both form the principle question and to help answer it. Both ponds are located within Acadia National Park on Mount Desert Island, Maine. Lake Wood is located on the north end of the island (44^{O} 24’ 28” N, 68^{O} 16’ 5” W, Figure 1), whereas The Bowl is on the east side (44^{O} 20’ 13” N, 68^{O} 11’ 36” W, Figure 1). Lake Wood is an 8-ha pond at an elevation of 45 m in a small vale among hilly lowlands on very stony sandy loam soils. The Bowl is an approximately 9-ha pond which lies in a perched depression in a mountainous area of the island, 417 m above mean sea level. The area around The Bowl has shallow, very gravelly, fine sandy loam soils and supported a mature red spruce (*Picea rubens*) forest prior to the great Bar Harbor Fire of October 1947 which burned the entire watershed of both Lake Wood and The Bowl. Both sites support maturing aspen-birch forests (with some oak and pine) today. A small hemlock stand occurs in the SW portion of the Lake Wood watershed. No hemlock occurs within The Bowl watershed..

CHAPTER 2

METHODS

Fuels Study

Fuel loadings in one modern, healthy (*i.e.*, currently unaffected by hemlock woolly adelgid) hemlock stand (Mount Toby Demonstration Forest) and one dead (and unsalvaged) hemlock stand (Devil’s Hopyard State Park) were sampled during late summer 2006. Modified Brown’s planar intercept sampling for downed woody fuels (Brown 1974) and harvest sampling for non-woody, fine fuels in 40 cm x 40 cm plots (after Woodall 1998 and Patterson *et al.* 2005) were employed to characterize fuel loads. Procedures used are detailed in Iwamoto (2005). In brief, ten sample points (plots and lines) were sampled for each site using a stratified random sampling system. For woody fuels, a random azimuth was generated along which a 15-m (50-ft) sample plane was established. All intersections of the sampling plane with dead, unrooted woody material 0.64 cm (0.25 inch) or greater in diameter below a height of 2.7 m (9 ft) were recorded in 10-hour, 100-hour, and 1000-hour time-lag size classes. Surface fuels are the primary contributor to fire spread, thus fuels above 2.7 m are not considered in the fire behavior prediction system (BEHAVE, Rothermel 1983). Fuel time-lag classes are fuel diameter classes indicating the rate at which fuel particles gain or loose moisture based upon the time-lag principle. Time-lag is the time required for a fuel particle to reach 63% of the difference between the initial moisture content and the equilibrium moisture content (Pyne *et al.* 1996). In practical terms, 1-hour fuels are those up to 0.64 cm (0.25 inch) in diameter (also known as “fine fuels”), 10-hour fuels are 0.64 cm to 2.54 cm (0.25 to 1.0 inch) in diameter, 100-hour fuels are 2.54 cm to 7.62 cm (1.0 to 3 inches) in diameter, and 1000-hour fuels are greater than 7.62 cm. “Heavy fuels” consist of 10-, 100-, and 1000-hour fuels. Items in the 100-hour and 1000-hour class were also measured for diameter and recorded as “sound” or “rotten”. Litter depth, slash depth, dead standing fuel height, and live standing fuel height, all components in the calculation of fuel bed depth, were measured at four systematically determined points along the sampling plane. Fuel bed depth is used along with fuel loadings to calculate the packing ratio. Packing ratio is the fraction of the fuelbed volume that is occupied by fuel particles (Scott and Burgan 2005) and is an important factor in predicting fire behavior.

From a randomly determined place near a Brown’s line, a 40 cm by 40 cm area was harvested for all litter, downed dead wood, and live and dead shrubs and herbs (humus was not harvested) and placed in separate paper bags. In the laboratory, contents of the bags were oven-dried to a constant weight at 70° C, and 1-hour fuels were separated into live wood, dead down wood, live herbs, live foliage, and litter (down, dead foliage) and weighed to the nearest 0.1 g. A variable radius plot was also measured at one end of each Brown’s line (results of which are presented in the description of the study sites).

The fine fuel loading data from the harvest plots and the heavy fuel loading data and the fuel bed depth variables from the planar intercept lines were used in the fire behavior calculations. Brown’s lines are line-intercept (fuel loads) and point-intercept (fuel bed depth) techniques designed to assess down woody fuels that ignores litter and other fine fuels. Small harvest plots provide assessment of fine fuels, but may underrepresent heavier fuels because of the small total area actually sampled. Using Brown’s lines for heavier fuels and fuel bed depth and small harvest plots for fine fuels compensates for the weakness of the Brown's lines in measuring fine fuels and the weakness in the harvest plots for measuring heavy fuels. Calculation of weighted average fuel bed depth was performed with Brown's line data.

Data from the Brown's lines were analyzed using equations presented in Brown (1974) using Microsoft Excel templates based on Brown's equations (Iwamoto 2005). Harvest plot data were extrapolated from g/1600 cm^2 to Mg/ha (metric tonne per hectare). Raw fuels data were entered and analyzed in Microsoft Excel templates (Iwamoto 2005) developed to generate fuel loadings and depths for further analysis.

Fuels data were used in the BehavePlus program (Andrews *et al.* 2002) to generate custom fuel models for the unaffected and affected stands. Burgan and Rothermel (1984) describe in detail the variables, equations, and procedures in generating custom fuel models. BehavePlus allows one to enter appropriate values for all the variables and generates custom fuel models based on the Rothermel equations. In addition to the fuels data collected in the field, certain other values that were not directly measured were borrowed from similar vegetation/fuels or determined from previous experience (*e.g.*, Patterson *et al.* 1983, Woodall 1998, Patterson 1999, Patterson 2001). These values include (Table 2) "static" for fuel model type, 100% for coverage, 6560 m^2/m^3 for 1-hour surface area:volume ratio, 6560 m^2/m^3 for live herbaceous surface area:volume ratio, 4920 m^2/m^3 for live woody surface area:volume ratio, 23% for dead fuel moisture of extinction, 9480 kJ/kg for dead fuel heat content, and 7900 kJ/kg for live fuel heat content. Note that fuel model type in BehavePlus is "static" or "dynamic." Dynamic fuel models have a live herbaceous fuel component, a portion of which is transferred into the dead herbaceous fuel load depending upon the live herbaceous fuel moisture content. Fuel models with no appreciable live herbaceous fuel component are static.

Burgan and Scott (2005) have developed a comprehensive set of Standard Fire Behavior Fuel Models (SFBFM) for use with the Rothermel (1983) surface fire prediction equations which form the basis of BehavePlus (Andrews *et al.* 2008). Using a key provided in Burgan and Scott plus fuel type, fuel loading data, fuel bed depth, moisture of extinction (the fuel moisture content above which fire spread ceases – higher values, around 25% or more, are more typical of the fire environment in the East), and expected fire behavior in the descriptions of the standard models (versus the predicted fire behavior from the custom models), the standard models which provide the closest approximation of the custom models were chosen.

Table 2: BehavePlus input sources and values.

variable	**source or value if constant (value underlined)**	**variable**	**source or value if constant (value underlined)**
fuel model type	Static	dead fuel moisture of extinction (%)	23
1-hour fuel load (Mg*/ha)	harvest plots	dead fuel heat content (kJ/kg)	9480
10-hour fuel load (Mg/ha)	Brown's lines	live fuel heat content (kJ/kg)	9480
100-hour fuel load (Mg/ha)	Brown's lines	1-hour fuel moisture (%)	6
live herbaceous fuel load (Mg/ha)	harvest plots	10-hour fuel moisture (%)	8
live woody fuel load (Mg/ha)	harvest plots	100-hour fuel moisture (%)	9
1-hour SA:V ratio (m^2/m^3)	6560	live herbaceous fuel moisture (%)	200
live herbaceous SA:V ratio (m^2/m^3)	6560	live woody fuel moisture (%)	150
live woody SA:V ratio (m^2/m^3)	4920	mid-flame windspeed (km/hr)	4.8
fuel bed depth (m)	weighted mean fuel bed depth	slope (%)	20

n.b. values were entered in "English" units; results were converted to metric units
* 1 Mg = 1 megagram = 1,000 kg = 1 metric tonne

BehavePlus was used to generate fire behavior predictions from both the custom and standard fuel models. A set of constant input parameters (Table 2) which are moderately severe but not exceptional in New England were used in combination with the custom and standard fuel models to generate fire behavior predictions. Although the standard models are not as accurate as the custom models in predicting fire behavior for the stands examined, they are presented in comparison with the custom fuel models for fire managers who may have access to the standard models but do not have the data to produce custom models.

Four measures of fire behavior were generated by BehavePlus: rate of spread, flame length, fire line intensity, and heat per unit area. Rate of spread is the rate at which a flaming front moves across a horizontal distance measured in meters per minute (m/min). Flame length is the distance in meters (m) measured from the tip of the flame to the middle of the flaming zone at the base of the fire. Fire line intensity is the rate at which heat energy is released per unit length of the flaming front expressed in kilowatts per meter (kW/m). Heat per unit area expressed in kiloJoules per square meter (kJ/m^2) is the heat released by a unit of area when that area burns (Rothermel 1983).

Fossil Pollen and Charcoal

A sediment core was recovered from Hawley Bog in February, 2006, using a 5-cm diameter, 2-m long plastic tube and piston corer. Cores from Round Pond and Larkum Pond were recovered in February, 2007, using a 5-cm diameter, 1-m long Livingstone corer. (See Cushing and Wright 1965 for coring device details.) At all three sites, cores were recovered from the frozen surface of the pond, at the deepest part of the pond as determined by weighted lines and an electronic depth finder. The Hawley Bog core was left *in situ* in the corer and extracted in the laboratory while the Round Pond and Larkum Pond cores were extracted in 1-m sections in the field, wrapped in plastic wrap and aluminum foil, and returned to the laboratory. In the laboratory, each core was initially sampled at intervals of 10- to 25-cm, and the samples were analyzed (procedure below) to determine the stratigraphic position of the hemlock decline in the core. Once the position of the hemlock decline was determined, approximately 1 m of the core encompassing the decline was sliced into one centimeter sections. From the center of each section, 0.5 cc samples were taken and analyzed for fossil pollen and charcoal at fine resolution intervals of 1-5 cm (after Green 1982) for 10-40 cm above and below the onset of the hemlock decline.

Processing of the sediment samples followed Faegri and Iverson (1975). One-half cubic centimeter of a suspension of non-native *Eucalyptus* pollen in glycerin (approximately 100,000 grains/cm^3 depending on the core) was added to each sample as a reference marker (explained below). Sediments were treated with 10% potassium hydroxide to dissolve humic compounds, 10% hydrochloric acid to dissolve carbonates, 48% hydrofluoric acid to dissolve silicates, and an acetolysis solution to remove organic residue other than pollen and charcoal. Residual material was suspended in silicone oil and mounted on microscope slides. Slides were examined at 400X with a Zeiss Standard light microscope.

A minimum of 300 fossil pollen grains were identified per sample. Fossil pollen grains were identified with the aid of illustrated keys (*e.g.,* McAndrews *et al.* 1973) and reference material in the collection of the Paleoecology Laboratory at the University of Massachusetts.

Several techniques have been used to quantify charcoal in sediments including point count or charcoal area estimation via light microscope, elemental carbon analysis, magnetic measurement of sediments, electron microscopy (primarily for enhanced identification and differentiation of source material), spectrographic analysis, and image analysis (Patterson *et al.* 1987, Foster *et al.* 2006). For this study, charcoal concentrations were quantified using the grid count method (Patterson *et al.* 1987), which estimates the surface area of charcoal fragments on microscope slides. The procedure, although time-consuming, is particularly convenient for fossil pollen analysis because additional processing beyond that for preparing sediments for fossil pollen analysis is not needed, and little specialized equipment besides that used for fossil pollen analysis is required (only a grid reticule for the microscope ocular lens). The procedure yields the ratio of charcoal area to numbers of fossil pollen grains (μm^2/gn) (see below), which is used as a measure of past fire occurrence on the landscape. The use of a ratio rather than absolute area measurement places the charcoal data within the same relative frame of reference as the pollen data (as with pollen, absolute charcoal numbers can be calculated if sufficient time reference points are available to calculate sediment influx rates, Swain 1978). It is not practical to identify and count pollen grains and measure charcoal area simultaneously. While pollen and spore grains are being counted, *Eucalyptus* grains are also counted and a fossil pollen grain to *Eucalyptus* grain ratio is calculated. As slides are re-examined for charcoal area, *Eucalyptus* grains are counted again and a charcoal area to *Eucalyptus* grains ratio is calculated. The charcoal area to pollen grain ratio can then be calculated by dividing the charcoal:*Eucalyptus* ratio by the pollen:*Eucalyptus* ratio.

Charcoal:pollen ratios in lacustrine sediments dating to high-intensity landscape-scale fires have peaks that are generally 250 to 500 and sometimes exceed 1,000 or more. Patterson *et al.* (2005) suggest that for lake sediments in basins that receive surface water runoff, charcoal:pollen values exceeding 500 – 1000 represent local fires or, in the case of wetlands, fires burning through the wetland itself. Motzkin *et al.* (1993) further support this idea in a study of an Atlantic white cedar (*Chamaecyparis thyoides*) swamp where very high charcoal:pollen ratios (up to almost 27,000) are contemporaneous with cedar nadirs suggesting stand-replacing fires passing over and through the wetland. In 1947 a large fire burned 27% of Mount Desert Island, Maine. Charcoal:pollen ratios for samples at the time of the fire for The Bowl, which lies entirely within the burned area, reach 800 while charcoal values from other depths do not generally exceed 400 (Patterson *et al.* 1987). Sergeant Mountain Pond which lies just a few hundred meters outside of the burn area has no charcoal peaks at the depth corresponding to the fire (Patterson *et al.* 1987). Charcoal:pollen ratios of up to 500 may represent regional fire activity. Although measured in charcoal accumulation rates rather than the pollen:charcoal ratio used in this study, Clark and Patterson (1997) concluded that peaks in charcoal above the “background” levels indicated local (*i.e.*, within the watershed of the deposition basin) fires while the “background” charcoal abundances indicated fires occurring regionally.

Approximate dates for sections of the cores were determined by cross-referencing certain changes in pollen percentages in the core to ecological events of known dates. The most useful dating tool in this study, as it is present in all five cores, is the onset of hemlock decline itself which dates to about 5,500 calendar years B.P. Other events of use in at least some of the cores are the arrival in southern New England of chestnut approximately 2,000 years B.P. and the arrival of hickory approximately 7,000 years B.P. (Williams *et al.* 2004). Some dates (*e.g.*, top and bottom of diagram) were extrapolated from sedimentation rates calculated based on the other markers, but should be considered only very approximate as this method assumes sedimentation rates are constant which is rare in reality. Chronostratigraphy was confirmed for one core, Round Pond, through the use of ^{14}C dating.

The pollen analysis program, TILIA (Grimm 1993), along with TILIA's graphic counterpart, TGView (Grimm 2004), were used to analyze the sediment data and generate pollen and charcoal diagrams.

In addition to pollen and charcoal diagrams, the pollen data were subjected to multivariate analysis, specifically ordination, to graphically represent the dataset in a way that may be easier to illustrate vegetation trends. Through ordination major ecological trends or patterns of variation among samples and entities (the samples representing points in time and the pollen types, in this case) are described. Ordination simplifies the complexity of the dataset by organizing sampling entities along gradients (axes) defined by combinations of interrelated variables (McGarigal *et al.* 2000). Detrended correspondence analysis (DCA), an unconstrained ordination technique, was chosen as the best technique to use on the data. Detrended correspondence analysis is derived from reciprocal averaging which simultaneously ordinates the rows (samples) and columns (species) of the dataset. DCA applies two additional steps beyond reciprocal averaging: detrending and rescaling to minimize the "arch effect" and axis compression. Unlike many other ordination techniques such as principal components analysis and polar ordination, the dual species and samples ordination of DCA produces a “joint plot” of ordinated species and samples which is useful in visualizing relationships between the two. A constrained technique, such as canonical correspondence analysis was not employed because there was no set of environmental or other “constraining” variables.

Beyond the advantage of simultaneous ordination of samples and species, DCA has further advantages. It maximizes the correlation between sample and species scores, can handle large complex datasets, and is particularly suited to data which are distributed in a nonlinear fashion (*i.e.*, not along a gradient). Disadvantages include that DCA is sensitive to outliers and discontinuities in the data, does not ordinate the species as accurately as the samples, and ordination of the second and successive axes are less robust than on the first axis (McGarigal *et al.* 2000).

All taxa with pollen percentages <2% in all samples were removed from the dataset. This procedure helped to minimize analysis problems with rare taxa and zeroes in the dataset, limited the analysis to those variables which have the most ecological influence, increased the consistency of the analysis across sites and simplified interpretation of the graphs by reducing the number of species points. This left all datasets with seven taxa: hemlock, pine, birch, oak, beech, ash, and sugar maple (referred to as “maple” on the scatterplots to conserve space). Fortuitously, these same taxa are those which are most important to identifying responses to hemlock decline, because they are either early successional (birch and to a lesser extent pine and ash) taxa, competitors of mature hemlock (oak, sugar maple, beech), or may indicate a response to changes in fire regime (pine, oak, maple, beech).

The DCA was run using PC-ORD, a multivariate analysis program (McCune and Mefford 1999), with axes divided into 26 detrending segments and axes rescaled with a threshold of 0. DCA results were graphed twice for each dataset: on a joint plot that includes species and samples together showing the relationship of species and sample ordinations relative to each other, and on a scatterplot of samples only which facilitates visual interpretation of the samples' ordination. To the graph of the samples, successional vectors were added connecting adjacent samples. Polygons were drawn around groups of samples which are related especially in terms of hemlock pollen patterns, and pollen trends within and among these groups are annotated on the graphs.

CHAPTER 3

RESULTS

Fuels Study

Fuel loads and fuel bed depth were consistently higher in the adelgid affected stand than the unaffected stand (Table 3). For example, the total mean fuel load for the unaffected stand was 39.6 Mg/ha while the fuel load for the affected stand was 107 Mg/ha (Table 2). Similarly, the weighted mean fuel bed depth was 6.1 cm for the unaffected stand and 18.3 cm for the affected stand (Table 3). For fine (1-hour) fuels, which are most important to the spread of surface fires, fuel load in the unaffected stand was 8.2 Mg/ha and 12.4 Mg/ha in the affected stand. In terms of fire behavior, the affected stand has higher values for all four variables than the unaffected stand (Table 4).

Although none of the standard models matched the custom models well, the closest fits from among the standard models are model TL2 (“timber litter model 2”) for the unaffected stand and model SB2 (“moderate-load slash model 2”) for the affected stand (Scott and Burgan 2005). TL2 and SB2 were selected because they have fuel types, fuel loadings, fuel bed depths, moistures of extinction, and predicted fire behavior most similar to the custom fuel models, respectively (Tables 3 and 4).

Table 3: Fuel loadings and fuel bed depths for unaffected and affected hemlock stands.

variable	**unaffected**	**affected**	**SFBFM TL2**	**SFBFM SB2**
fuel type	litter under forest canopy	litter and slash under partial or low canopy	litter under forest canopy	slash
mean 1-hr fuel loads (Mg/ha)	8.2	12.4	3.1	10.1
mean 10-hr fuel loads (Mg/ha)	3.6	7.2	5.1	9.5
mean 100-hr fuel loads (Mg/ha)	3.0	9.8	4.9	9.0
mean 1000-hr fuel load (Mg/ha)	24.8	77.6	N/A*	N/A*
total mean fuel load (Mg/ha)	39.6	107.0	N/A*	N/A*
weighted mean fuel bed depth (cm)	6.1	18.3	6.1	30.5
moisture of extinction (%)	23	23	25	25

* SFBFM do not consider 1000-hour fuels

Table 4: Predicted fire behavior as calculated by BehavePlus.

variable	**unaffected**	**affected**	**TL2**	**SB2**
rate of spread (m/min)	0.23	1.55	0.26	2.9
flame length (m)	0.21	0.91	0.21	1.43
fireline intensity (kW/m)	9.0	206	8.0	564
heat per unit area (kJ/m²)	2625	8240	1639	11372

To further illustrate the differences in fire behavior between the affected and unaffected stand, custom fuel models were generated and fire behavior predicted for each plot individually (Table 5). These data were then sorted into rate of spread and flame length classes. Both affected and unaffected stands' data were graphed as frequency distributions for rates of spread and flame lengths (Figures 2 and 3, respectively). At no point do the frequency distributions of either the rates of spread or flame lengths overlap. Note also that 99% confidence intervals do not overlap between affected and unaffected stands for either rates of spread or flame length. The rates of spread and flame lengths between the affected and unaffected stands are significantly different (p=.01) (Table 6, Figure 4). The results suggest that stands which have recently suffered severe hemlock declines will burn more intensely than healthy hemlock stands.

Table 5: Fire behavior results for individual sample points.

unaffected			**affected**		
sample point	**rate of spread (m/min)**	**flame length (m)**	**sample point**	**rate of spread (m/min)**	**flame length (m)**
1	0.46	0.27	1	1.65	0.94
2	0.16	0.12	2	1.68	0.97
3	0.50	0.30	3	1.58	0.94
4	0.66	0.42	4	1.29	0.82
5	0.43	0.24	5	2.18	1.24
6	0.76	0.45	6	1.06	0.70
7	0.26	0.27	7	0.92	0.67
8	0.43	0.33	8	1.19	0.73
9	0.69	0.42	9	1.68	0.94
10	0.50	0.30	10	1.45	0.88

Figure 2: Frequency distribution for rates of spread of individual sample points.

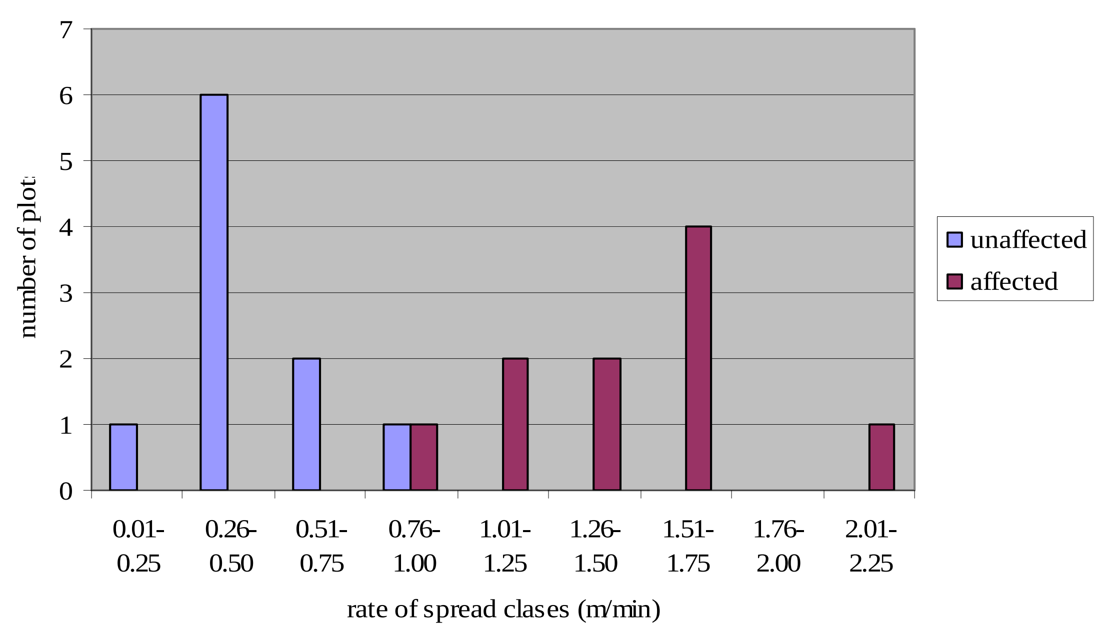


Figure 3: Frequency distribution for flame lengths of individual sample points.

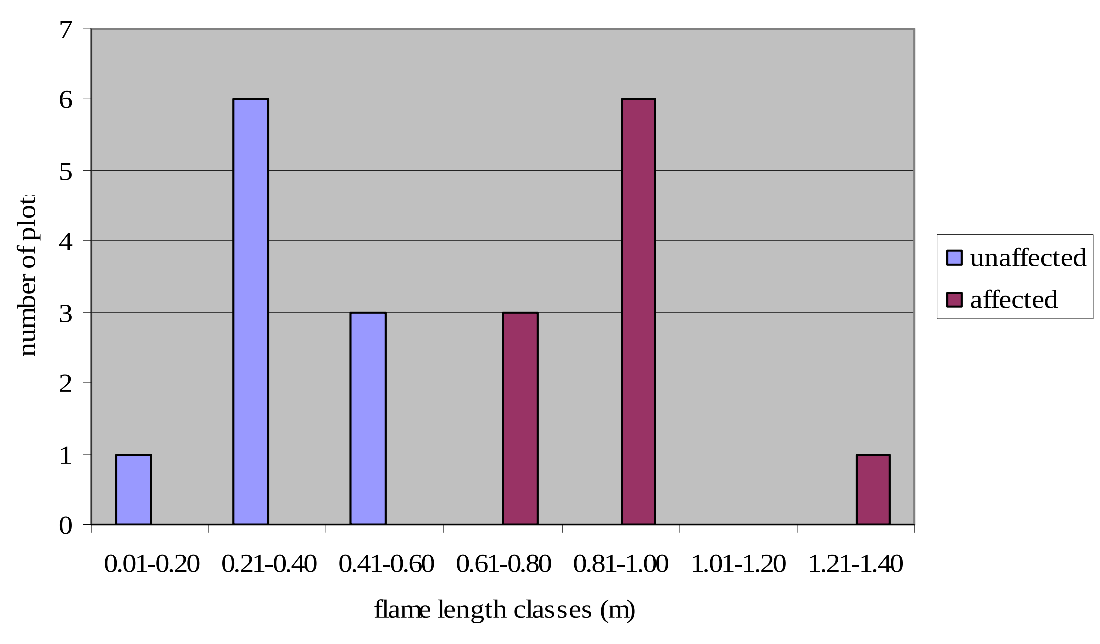
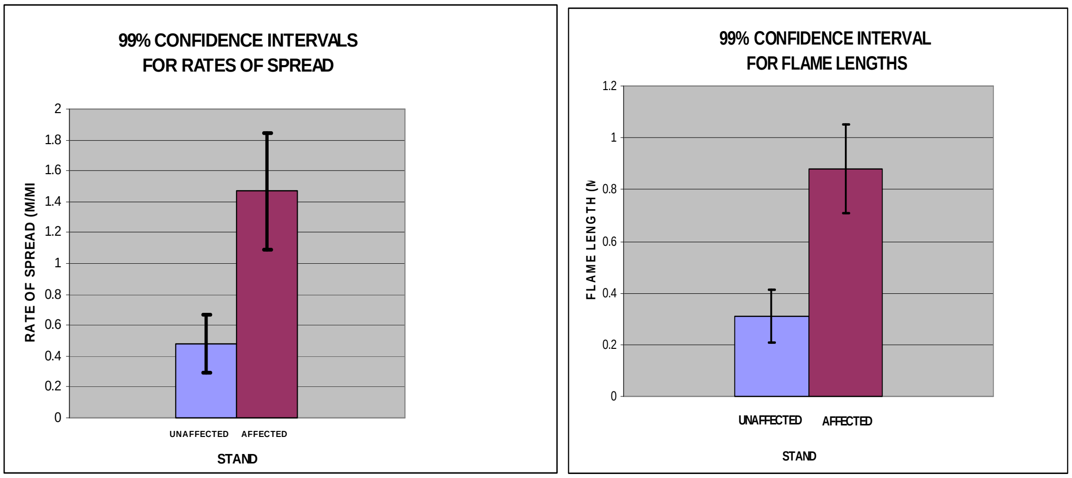


Table 6: 99% confidence intervals for means of individual sample points.

variable	**unaffected**	**affected**
rate of spread (m/min)	0.48±0.19	1.47±0.38
flame length (m)	0.31±0.10	0.88±0.17

Figure 4: 99% confidence intervals for means of individual sample points.



Sedimentation and Dating

Pollen and charcoal diagrams for the five sites summarize the vegetation and fire history for the period before, during, and immediately after the prehistoric hemlock decline (Figures 5 - 9). The sediment cores were 1.25 m, 5.0 m, and 6.0 m in length for Hawley Bog, Round Pond, and Larkum Pond, respectively. The sediment consisted entirely of dark brown gyttja in the Hawley Bog, Larkum Pond, and Round Pond cores with no mineral content detectable by palpation, no dark bands suggesting discrete layers of charcoal, and little to no fibric peat. Few macrofossils including charcoal fragments >1 mm in largest dimension were found during the sampling of the cores. Those that were found consisted almost entirely of rootlets which were probably of local origin. The Hawley Bog, Larkum Pond, and Round Pond cores were sampled at 28, 30, and 53 levels, respectively. Pollen and spores were generally well-preserved and readily identified, although nearly all of the pine pollen seen in the Round Pond sediments was

Figure 5: Fossil pollen and charcoal diagram for Hawley Bog.

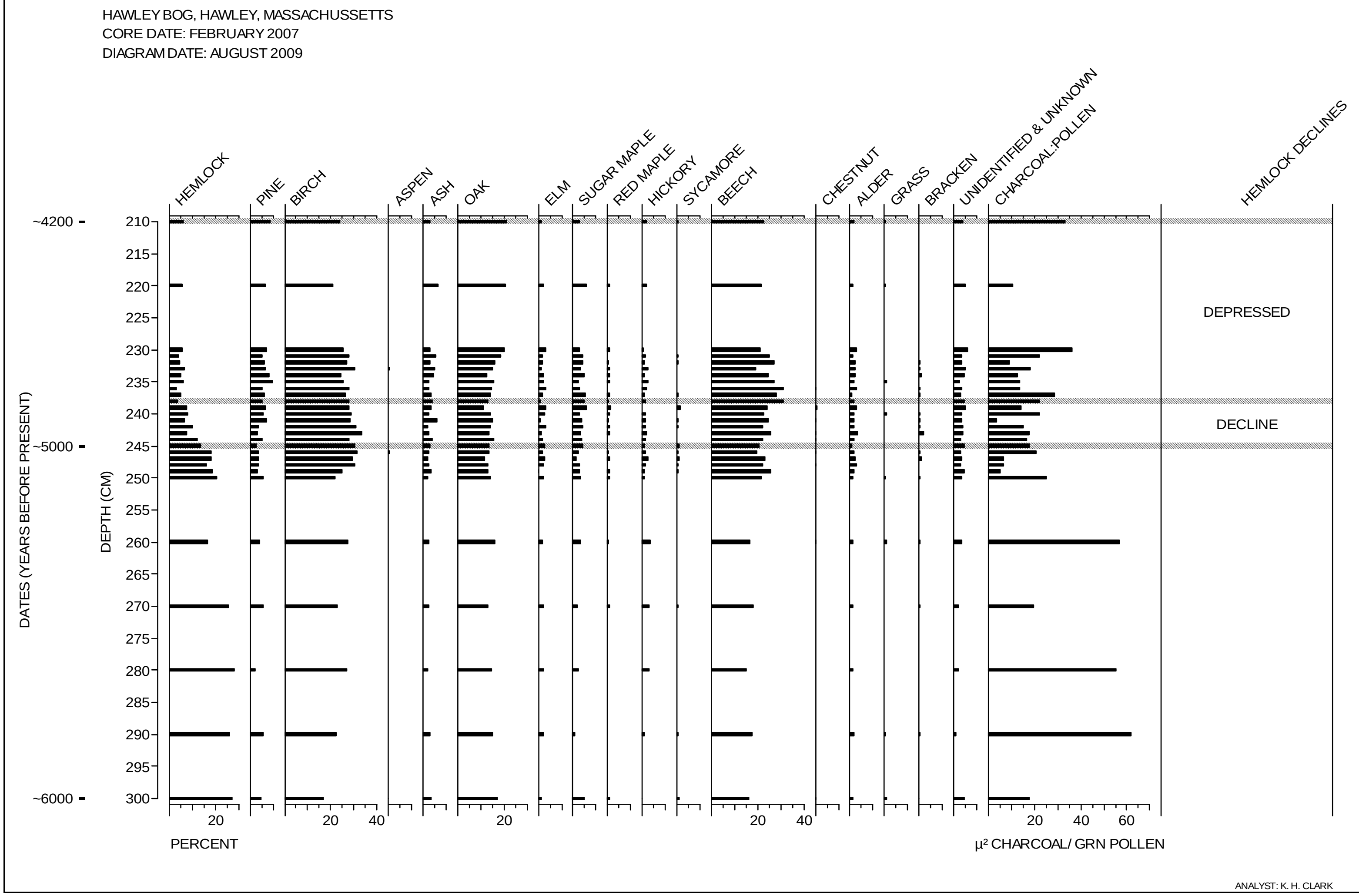


Figure 6: Fossil pollen and charcoal diagram for Larkum Pond.

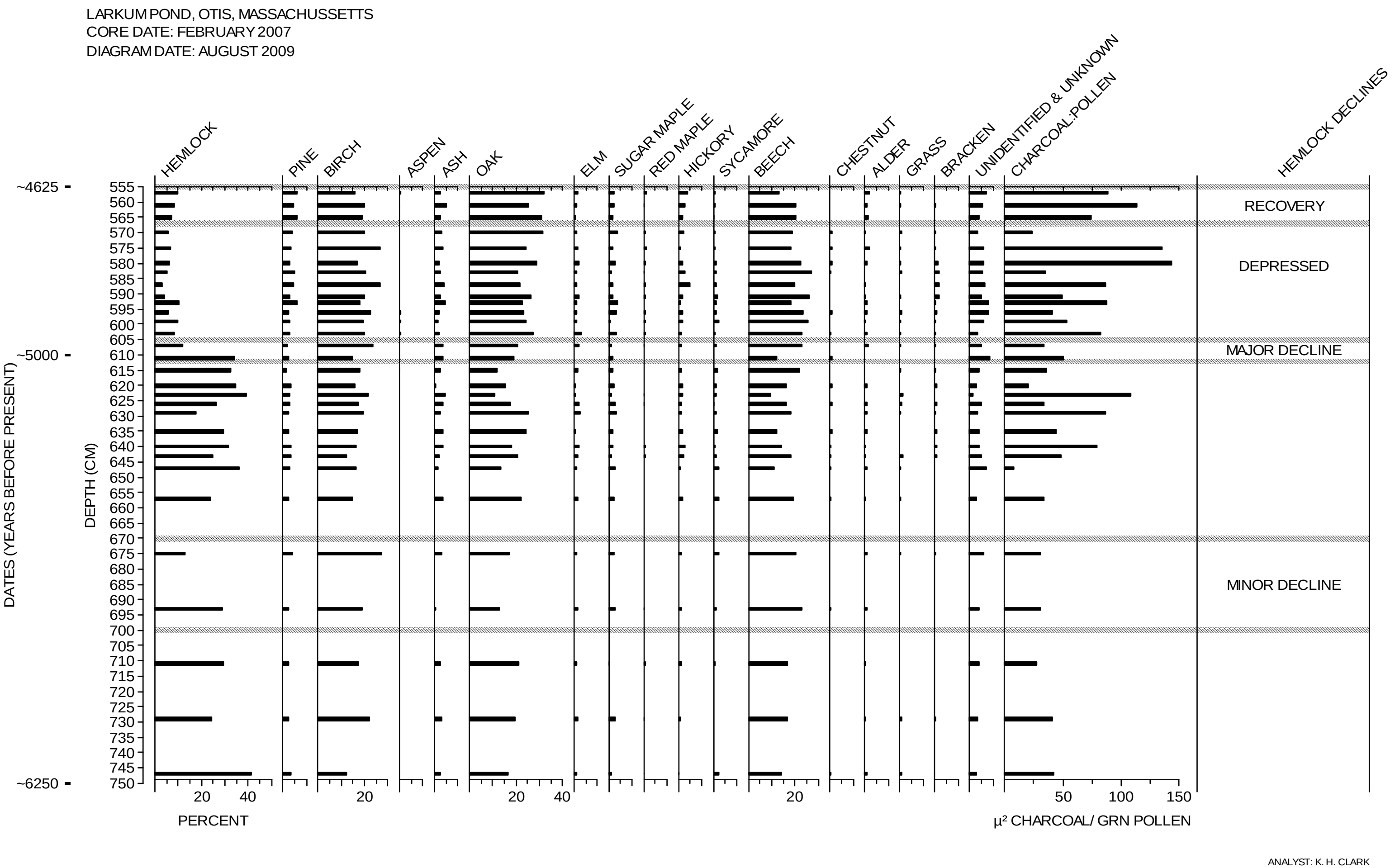


Figure 7: Fossil pollen and charcoal diagram for Round Pond.

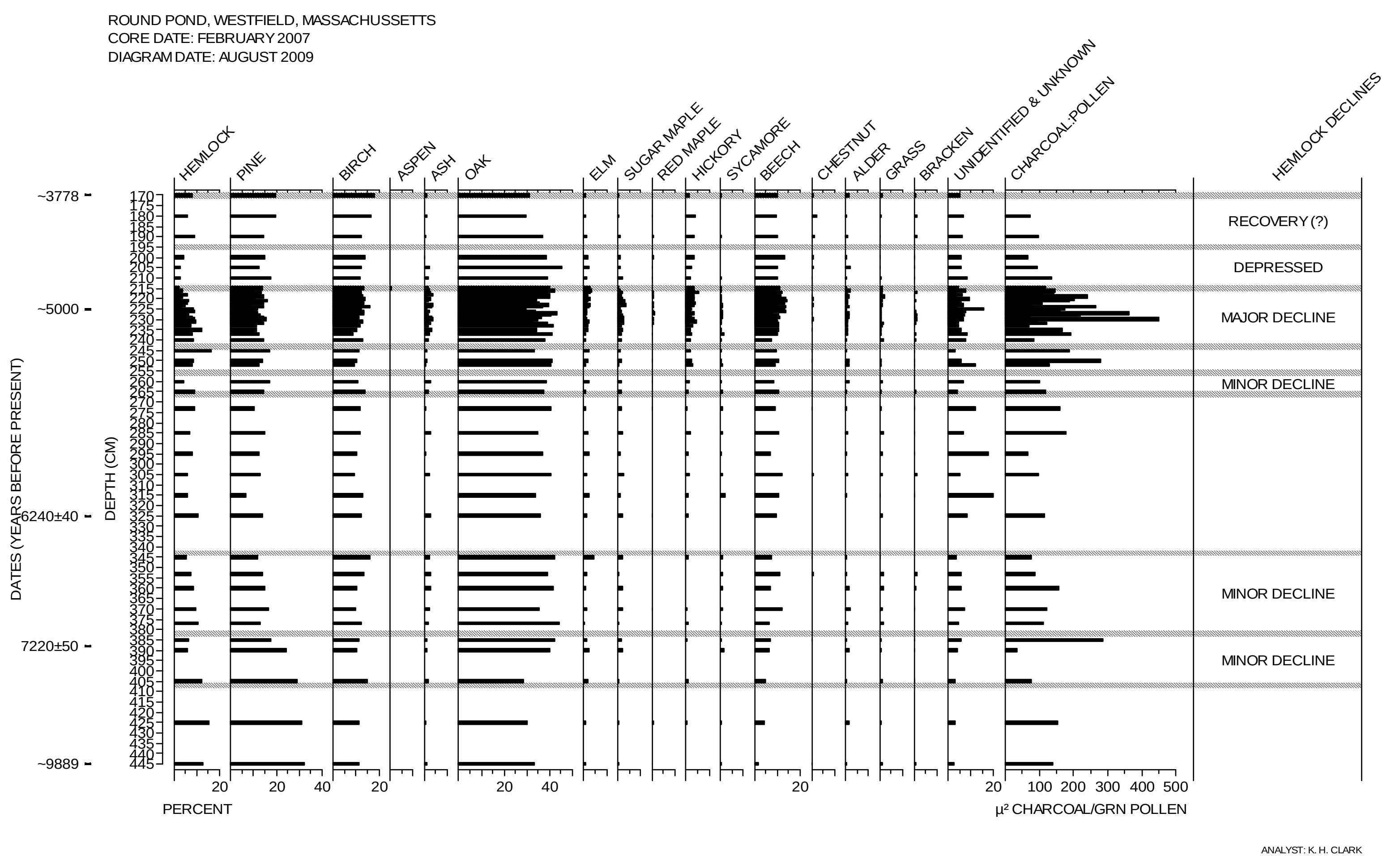


Figure 8: Fossil Pollen and charcoal diagram for The Bowl.

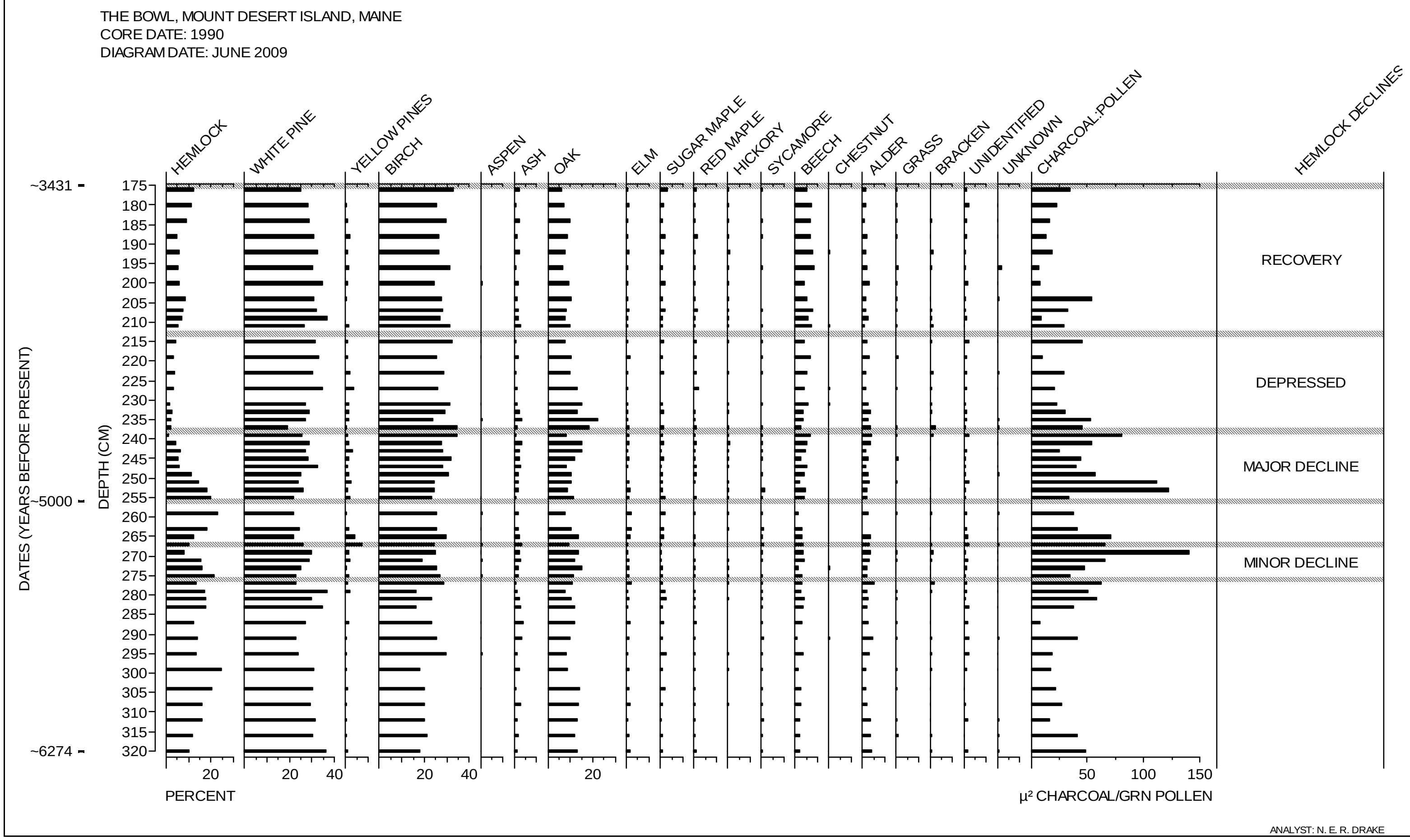
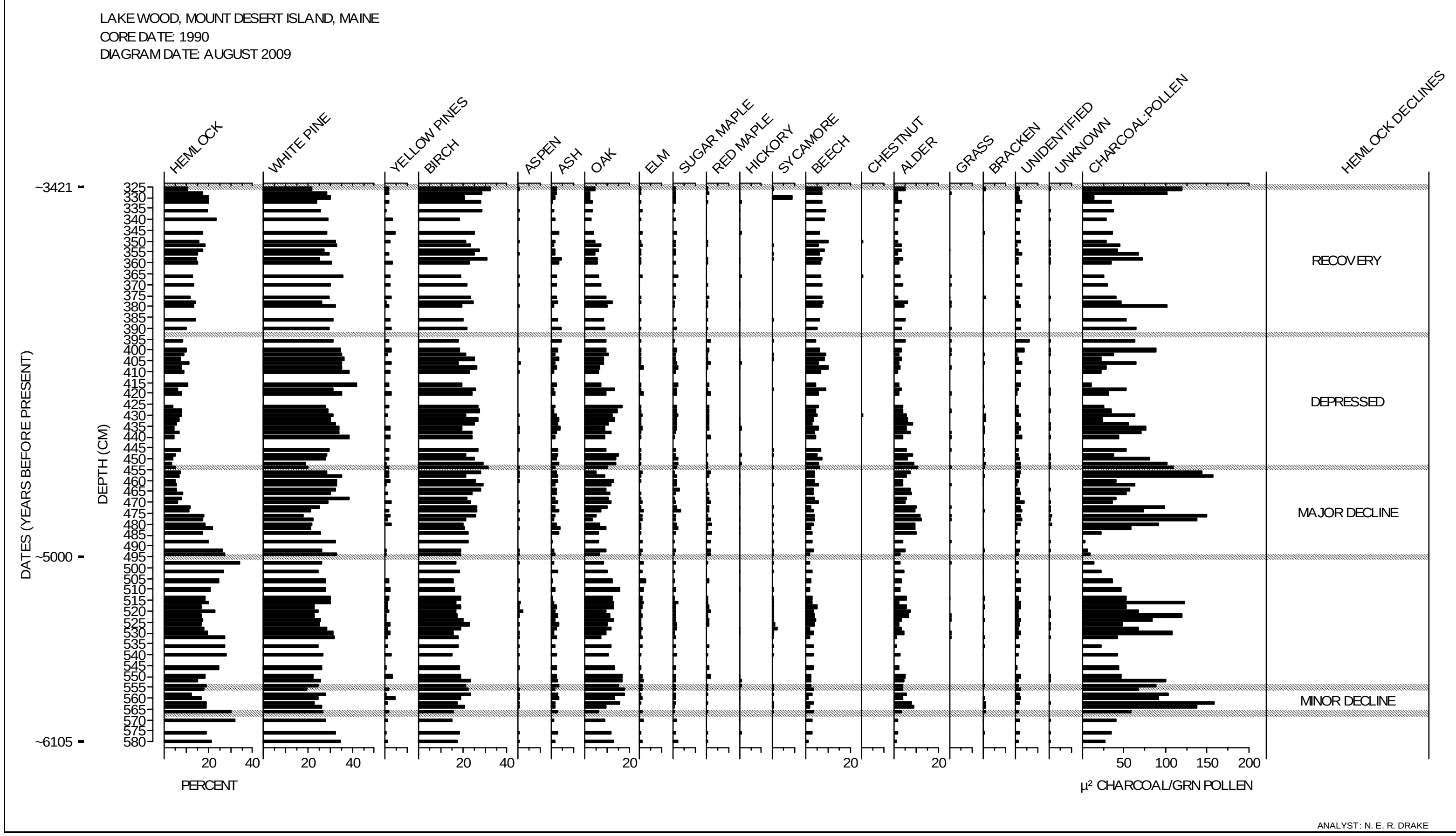


Figure 9: Fossil pollen and charcoal diagram for Lake Wood.



partially or completely torn and had to be counted using partial grain counting rules (Faegri and Iverson 1975). The mid-Holocene hemlock decline was readily apparent in the Hawley Bog and Larkum Pond sediments, but difficult to discern in the Round Pond core. Two samples from Round Pond, 325 cm and 388 cm, were submitted to Beta Analytic (Miami, FL) for Accelerator Mass Spectrometry ^{14}C radiocarbon dating analysis to assist with locating the hemlock decline. Sediment from 325 cm was dated at 6,240 ±40 ^{14}C yrs BP and from 388 cm at 7220 ± 50 ^{14}C yrs BP in conventional radiocarbon age, both prior to the most currently accepted date of 4750 ^{14}C yrs BP (approximately 5500 calendar yrs BP) for the hemlock decline (Bennet and Fuller 2002). Average sediment accumulation rates calculated from stratigraphic markers in the cores are approximately 0.5 mm/yr for Hawley Bog and Round Pond and approximately 1.2 mm/yr for Larkum Pond. Based on these estimated accumulation rates, the Hawley Bog diagram spans approximately 1800 years (6000 ^{14}C yrs BP – 4200 ^{14}C yrs BP), the Larkum Pond diagram 1625 years (6250 ^{14}C yrs BP – 4625 ^{14}C yrs BP), and the Round Pond diagram 6111 years (9889 ^{14}C yrs BP – 3778 ^{14}C yrs BP). Hawley Bog and Larkum Pond dates should be considered rough approximations, as they are not confirmed by radiocarbon dating and the calculations were performed with the assumption that the sedimentation rates are constant.

Each sample was drawn from the entire thickness of a one centimeter thick slice of the original core, therefore the Larkum Pond samples represent approximately 8 years of sediment accumulation, whereas the Round Pond and Hawley Bog samples represent approximately 20 years. To yield high resolution data, samples were taken every 1 cm (*i.e.*, continuously) from the parts of the Hawley Bog and Round Pond cores spanning the

4750 ^{14}C yrs BP hemlock decline, thus the sampling resolution for these cores is about 20 years. Because of its higher sedimentation rate, samples were taken only every 2 – 5 cm for the Larkum Pond core yielding a sampling resolution of 25 to 42 years. The span of high resolution sampling was 20 cm or approximately 408 years at Hawley Bog, 95 cm or approximately 791 years at Larkum Pond, and 25 cm or approximately 555 years at Round Pond.

The Lake Wood sediments accumulated at an estimated rate of 0.95 mm/yr, had a sampling resolution of 2 - 4 cm (mostly every 2 cm) or 21 - 42 years, and spanned approximately 2684 years (from 6105 ^{14}C yrs BP to 3421 ^{14}C yrs BP). The Bowl diagram has an estimated sediment accumulation rate of 0.51 mm/yr, a sampling resolution of 2 - 4 cm (mostly 4 cm) or 39 - 78 years, and covers a period of 2843 years (6274 ^{14}C yrs BP to 3431 ^{14}C yrs BP).

Hickory and chestnut are included on the diagrams in part for their value as stratigraphic markers for the southern New England sites (Hawley Bog, Larkum Pond, and Round Pond). Hickory migrated into southern New England around 7,000 ^{14}C yrs BP and chestnut not until almost 2,000 ^{14}C yrs BP (Williams *et al.* 2004). Since the range-wide, mid-Holocene hemlock decline occurred at 4750 ^{14}C yrs BP, hickory should be present at greater than 1% and chestnut should be absent (or at least less than 1%; a few grains may have reached the sediment basin via long-range transport) in samples corresponding to the hemlock decline. This is, in fact, the case for all three southern New England diagrams. Hickory and chestnut were never present locally at the Mount Desert Island sites.

Charcoal:pollen ratios are presented on the respective diagrams for each site (Figures 5 through 9). The abundance of charcoal varies greatly in all five cores. This is expected, as charcoal is generated from fires whose frequency, severity, and distance from the coring site varies from one site to the next, and at different times at the same site (Patterson and Backman 1988).

Vegetation History in Relation to Hemlock Decline

Definitions

The term "peak" is used in this study to describe an increase in pollen percentage or charcoal:pollen ratio which is short-lived (one to three levels). The term for the opposite situation is "nadir."

Several zones (ranges of levels) related to hemlock pollen percentages can be identified on the pollen diagrams. For purposes of this study, any zone in which hemlock percentages decrease by $\geq$50% (not 50 percentage points, but a 50% relative change in the pollen percentages) is considered a hemlock decline. If hemlock percentages drop to 5% or less for at least one level and remain <10% for an extended period, this zone is termed the "major hemlock decline" and represents the range-wide, mid-Holocene decline of 4750 ^{14}C yr BP. The major hemlock decline is further confirmed in the diagrams by chronostratigraphic markers and, in the case of Round Pond, by radiocarbon dating. Any decrease in hemlock pollen percentages that exceeds the 50% rule, but does not drop to <5% and remain <10% for an extended period is referred to as a "minor hemlock decline." The term "pre-decline" is used for all zones (including minor declines) occurring prior to the major decline. A range of levels following (*i.e.*, above) the major decline in which hemlock remains at low levels is the "depressed hemlock period." Note that in this study the major decline includes the levels in which hemlock percentages are decreasing, and the depressed hemlock period includes levels in which the hemlock percentages are consistently low following the major decline zone. A range of levels shallower (*i.e.*, more recent) than the depressed hemlock period in which hemlock percentages rise is called the "recovery period." Not all the diagrams have all these zones.

General Patterns of Hemlock Decline

Hemlock reached southern New England around 8,000 ^{14}C yr BP, experienced a precipitous decline at 4750 ^{14}C yr BP, and recovered to near previous levels at some sites by around 3,000 ^{14}C yr BP. This study focuses on a period from approximately 6,000 to 7,000 ^{14}C yr BP until 3,500 to 4,500 ^{14}C yr BP encompassing the period when hemlock at its peak distribution and abundance (during the Holocene) before the major decline, the major decline itself, all or some part of the depressed hemlock period, and (in some cores) the beginning of the recovery. The levels representing the various zones (pre-decline, major decline, depressed period, *etc.*) are delineated on the diagrams (Figures 5 through 9).

Hawley Bog

Hemlock pollen is steady at ≈25% before the decline. There are no minor declines. After a small decrease from ≈26% to 15%-20%, the major hemlock decline begins at 245 cm as hemlock decreases to ≈5%, then is <10% for the remainder of the diagram representing the depressed hemlock period. Oak, birch, and beech are other dominant taxa in the pollen profile. Oak remains steady at ≈15% before and during the decline, then increases to ≈20% after the decline. Birch fluctuates between 15% and ≈25% before the decline, increases to 30% - 35% during the major decline, and settles at

20% - 25% following the decline. Beech averages ≈15% before the major decline, fluctuates with increases as high as 32% during and immediately following the major decline and remains steady at ≈20% later during the depressed period. Pine is <5% before the major hemlock decline, and increases to 5% - 10% after the decline. Sugar maple, a partly insect pollinated (Burns and Honkala 1990) northern hardwood species common in the vicinity of Hawley Bog today, is at low levels (<10%) throughout the diagram, but increases from <5% before the major decline to >5% during and after the decline. Certain herbaceous taxa can indicate disturbance. For example, grasses are generally adapted to open or sunny conditions, and bracken fern spreads rhizomatously into shaded or partly-shaded disturbed areas. Grass pollen occurs only at very low levels (<1%) throughout the diagram. Bracken remains at ≤0.5% for most of the diagram except at 243 cm, immediately after the major decline onset, where it jumps to 1.9%, an almost 300% relative increase. Summarizing these changes in response to the major hemlock decline, birch and beech initially increased but then fell during the depressed period, oak and pine increased during the depressed period, sugar maple increased both during the major decline and the depressed period, and bracken fern peaked during the major decline.

Larkum Pond

At Larkum Pond, from 700 cm to 670 cm, hemlock experiences a minor decline from ≈30% to 15%, but percentages quickly rise again to 30% - 40%. The major hemlock decline is most precipitous at this site as hemlock falls from 34% to 12% between two levels (611 cm to 607 cm). Hemlock percentages remain depressed fluctuating from 3% - 10% until 561 cm where hemlock begins to recover. Like Hawley Bog, birch, oak, and beech are co-dominant pollen taxa at this site. Oak increases during the major decline, the depressed period, and the recovery, whereas birch, beech, and pine experience a few small peaks above their “background” levels during the depressed and/or recovery periods. Birch fluctuates from 15% - 25% across the entire core without an apparent pattern. There are two peaks in birch to 27% (575 cm and 587 cm) during the depressed period, but a peak to 27% is also reached at 675 cm during the pre-decline period. Oak ranges from 15% - 25% before the major decline, and increases to 20% - >30% during the major decline and the depressed hemlock period. Beech fluctuates from 15% - 25% on the diagram and has three peaks at 26% or 27% during the depressed period, but it has no level >23% before the major decline. Pine remains <5% for most of the core, but occasionally is >5% during the depressed and recovery periods (at 557, 565, 583, and 593 cm). With most of the other levels at 2% - 4%, an increase to >5% is a 50% to 100% relative increase in pine abundance. Sugar maple and elm both remain <5% across the diagram. Bracken is also present at very low levels, but does increase from essentially 0% at the lower levels to 1% - 2% during two periods, one before the major decline and one during the depressed period. Both of these increases correspond with increases in charcoal.

Round Pond

The major hemlock decline was difficult to discern in the Round Pond core, as hemlock percentages are <20 and there are several minor declines. Those at 400 cm and 350 cm were determined to be too old to be the major decline through the use of stratigraphic markers, the lack of a persistent “depressed period”, and ultimately the use of radiocarbon dating. Although the depth in sediment is roughly compatible with the major decline (*i.e.* 225 - 275 cm in most cores regionally), the minor decline at 260 cm was ruled out as the major decline because at approximately 200 years in duration, what would be the depressed period after that decline is brief (in paleoecological terms). The decline beginning at 245 cm was determined to be the major hemlock decline based on its position in the sediment and the longer persistence of very low ($\leq$5%) hemlock percentages. There appears to be a short depressed period from 195 cm - 215 cm and the beginning of a recovery above 195 cm, although this may simply be a slightly less depressed period as hemlock percentages do not exceed 10%. Oak is the dominant taxa in the Round Pond diagram with percentages ranging from 25% - 45%. There appears to be little pattern to the oak pollen fluctuations relative to hemlock (or charcoal) abundance except that the taxon reaches its peak (45%) at two levels: just after a minor hemlock decline at 377 cm and during the depressed hemlock period at 205 cm. Pine pollen is more abundant at Round Pond than at either Hawley Bog or Larkum Pond. Higher pine percentages are to be expected at Round Pond, as it is situated at the edge of a glacial outwash feature which currently supports extensive pitch and white pine stands. From ≈30% at the lowest levels of the diagram, pine percentages decrease to 10% - 15% during the first two minor hemlock declines where it remains until the recovery from the major hemlock decline at which point pine rises to 20%. Birch fluctuates from 10% - 15% throughout most of the core except during the hemlock recovery period when it exceeds 15%. Beech enters at 1.5% at the diagram's lowest level, 445 cm, then steadily increases over the next 6 levels to 12%, and then fluctuates from 7% - 14% over the rest of the diagram. These figures are consistent with the finding of Williams *et al.* (2004) that beech arrived in southern New England ca. 9,000 BP (approximately 405 cm on the Round Pond diagram). Peaks in beech (12% - 14%) occur both within and outside of hemlock declines on the diagram. Ash, elm, and sugar maple fluctuate from 1% - 4% throughout the diagram. Elm peaks occur during each minor decline and the major decline. Ash and sugar maple peaks seem to be patternless. In summary, Round Pond has the most minor declines and the least pronounced major decline of the sites examined. Oak, beech, ash, and sugar maple do not have a discernable pattern relative to declining hemlock; pine and birch abundances rise slightly during the recovery period; and elm experiences short-lived increases during hemlock declines.

The Bowl and Lake Wood

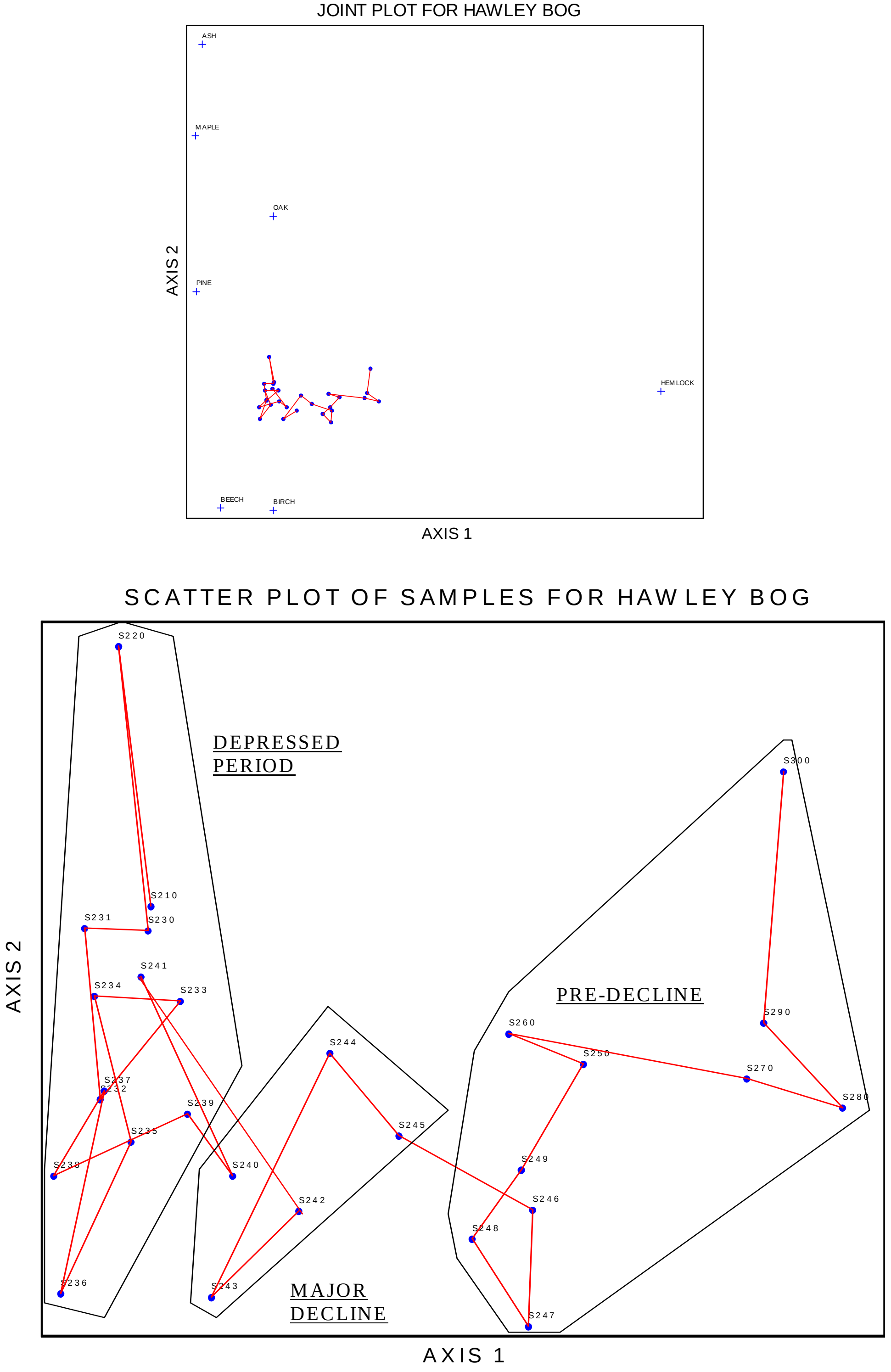
Although The Bowl and Lake Wood have different elevations, soils, hydrology, sedimentation rates, and modern vegetation, they lie in close proximity to each other (approximately 9 km distant), and, not surprisingly, have similar vegetation histories. Lake Wood generally has greater hemlock pollen (5% - 10% higher than The Bowl), but trends at both sites are similar. Hemlock decreases ca. 5,800 ^{14}C yr BP (300 cm for The Bowl, 565 cm for Lake Wood) and at 5,400 ^{14}C yr BP (275 cm for The Bowl, 530 cm for Lake Wood). Only the 5,400 ^{14}C yr BP decrease for The Bowl and the 5,800 ^{14}C yr BP decrease for Lake Wood meet the criteria for minor decline (*i.e*. they meet the 50% rule defined above). During the major hemlock decline (beginning at 255 cm for The Bowl, 495 cm for Lake Wood), Lake Wood hemlock pollen percentages drop to <5% for only a few levels but remain <10% for an extended period, whereas at The Bowl they remain <5% through most of the depressed period. White pine, birch, and hemlock are co-dominant at both sites and occur at similar abundances. White pine fluctuates between 20% - 35% and birch between 15% - 30% on both diagrams. Both The Bowl and Lake Wood have small peaks in birch at the latter part of the major hemlock decline. While

Lake Wood generally has more hemlock, The Bowl generally has more oak, which ranges from <10% to >20% compared to <5% to <20% at Lake Wood. At both sites, oak fluctuates during the pre-decline period, sometimes increasing with decreasing hemlock, and then experiences a small peak during the depressed period followed by a slight but steady decrease during the hemlock recovery. Beech increases beginning at the depressed hemlock period through the recovery period at both sites. Beech at both sites peaks at ≈10%.

Multivariate Analysis

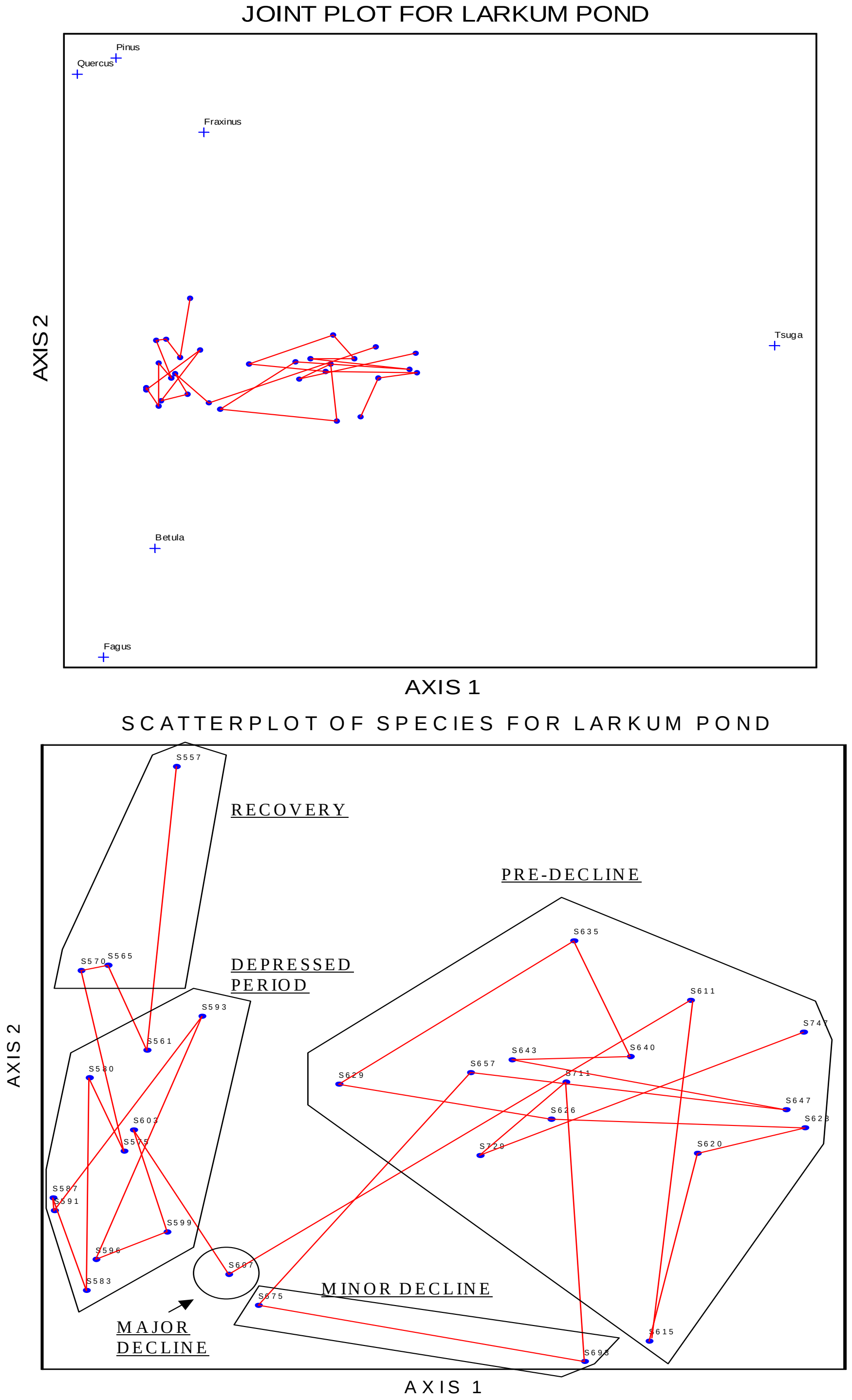
The results of the detrended correspondence analysis were graphed on two plots, one joint plot showing species and samples on the same graph and one scatterplot showing samples alone for each fossil pollen dataset (Figures 10 - 14). The samples-only scatterplots were graphed separately because the samples on the joint plots were too crowded to interpret visually. Use the joint plots to understand the relationship of the species to the axes and the samples-only scatterplots with successional vectors to discern changes in pollen type composition and follow the pollen composition through time. Note that hemlock ordinated strongly (far to the right) on axis 1 for all five sites so that samples that ordinate to the right on axis 1 are rich in hemlock and those that ordinate to the left are hemlock-poor (relative to overall hemlock pollen abundance at that site). Hemlock loaded heavily on the first axis from $r = 0.79$ (Round Pond) to $r = 0.99$ (Larkum Pond). Also, the first axis accounts for much of the total variance in the data set from 66% (The Bowl) to 92% (Larkum Pond). Both the high hemlock loadings on axis 1 and the large amount of total variance accounted by axis 1 reflect hemlock's being at least very common if not co-dominant at all the sites and the fact that hemlock experiences the greatest change of any of the pollen types (the major decline).

Figure 10: Detrended correspondence analysis for fossil pollen from Hawley Bog.



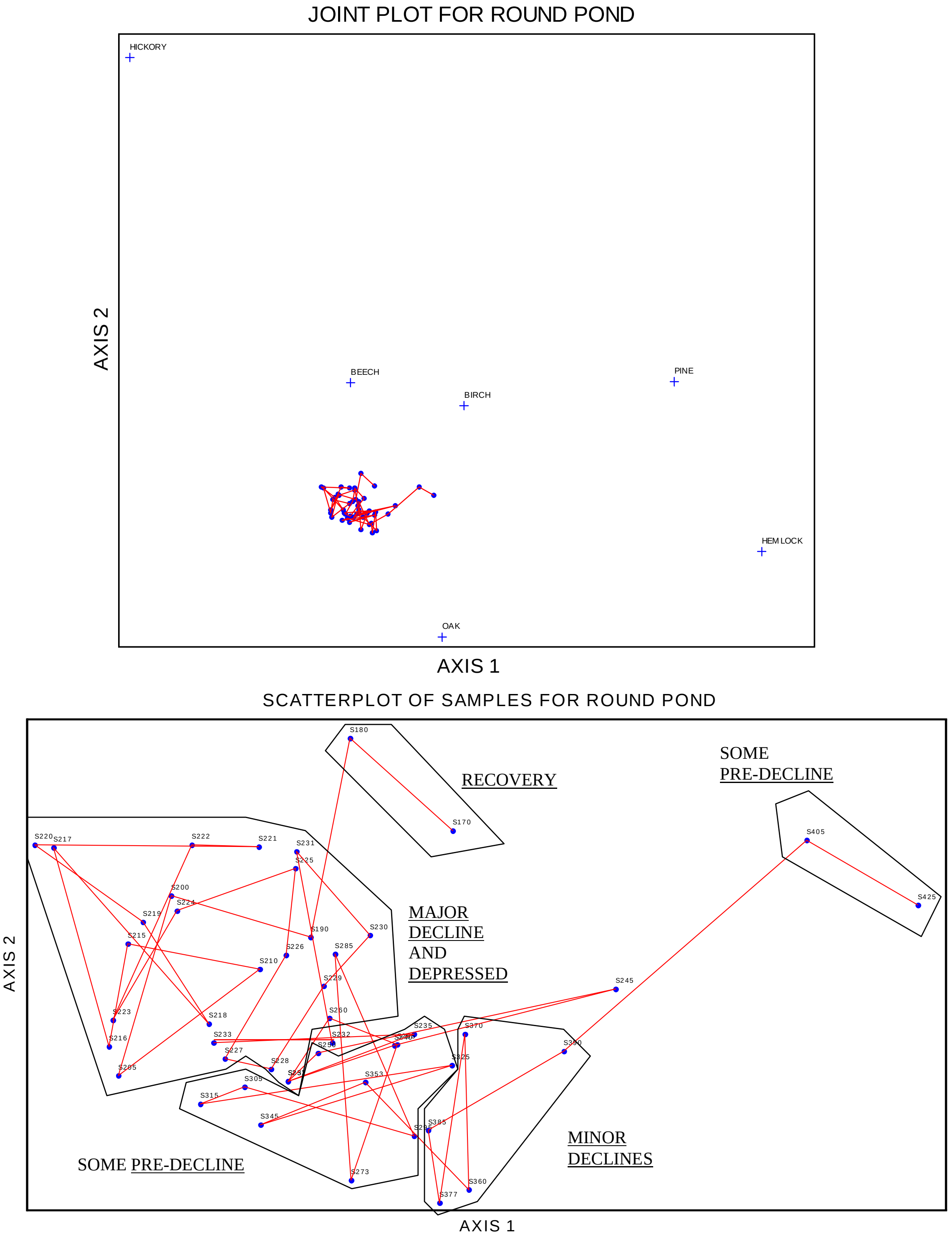
Top joint plot is species data (+) and sample data (●) graphed on the first two ordination axes. Red lines are successional vectors connecting adjacent levels. The bottom scatterplot is sample data only to better illustrate successional vectors and includes polygons which encompass groups of samples corresponding with zones on pollen diagrams.

Figure 11: Detrended correspondence analysis for fossil pollen data from Larkum Pond.



Top joint plot is species data (+) and sample data (●) graphed on first two ordination axes. Red lines are successional vectors connecting adjacent levels. The bottom scatterplot is sample data only to better illustrate successional vectors and includes polygons which encompass groups of samples corresponding with zones on pollen diagrams.

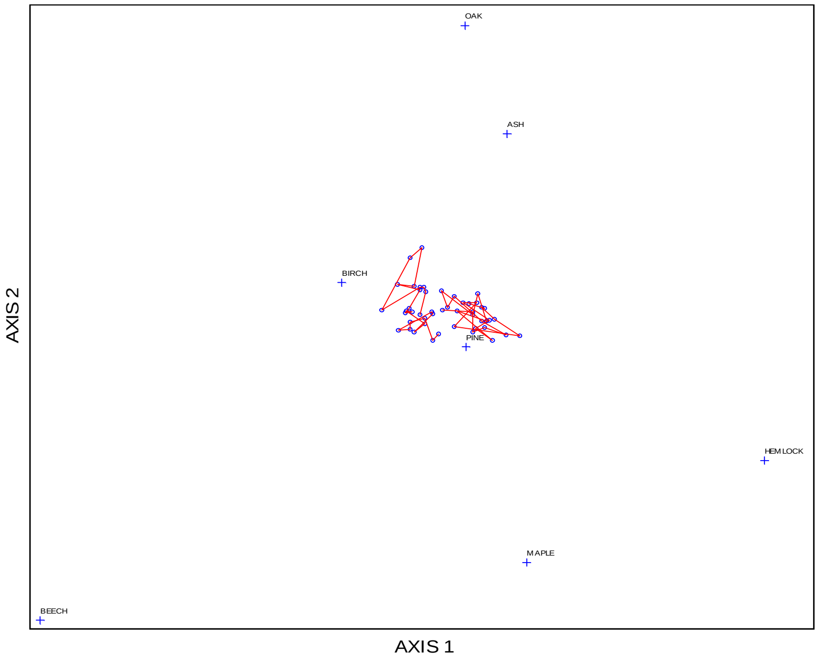
Figure 12: Detrended correspondence analysis for fossil pollen data from Round Pond.



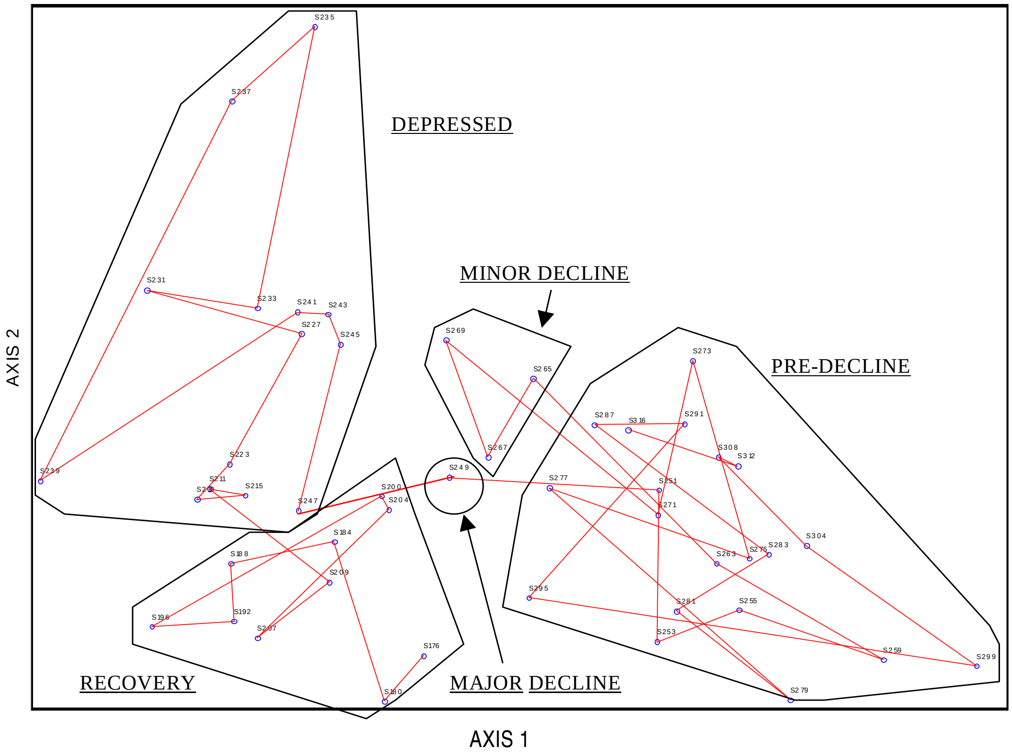
Top joint plot is species data (+) and sample data (●) graphed on first two ordination axes. Red lines are successional vectors connecting adjacent levels. The bottom scatterplot is sample data only to better illustrate successional vectors and includes polygons which encompass groups of samples corresponding with zones on pollen diagrams.

Figure 13: Detrended correspondence analysis for fossil pollen data from The Bowl.

JOINT PLOT FOR THE BOWL

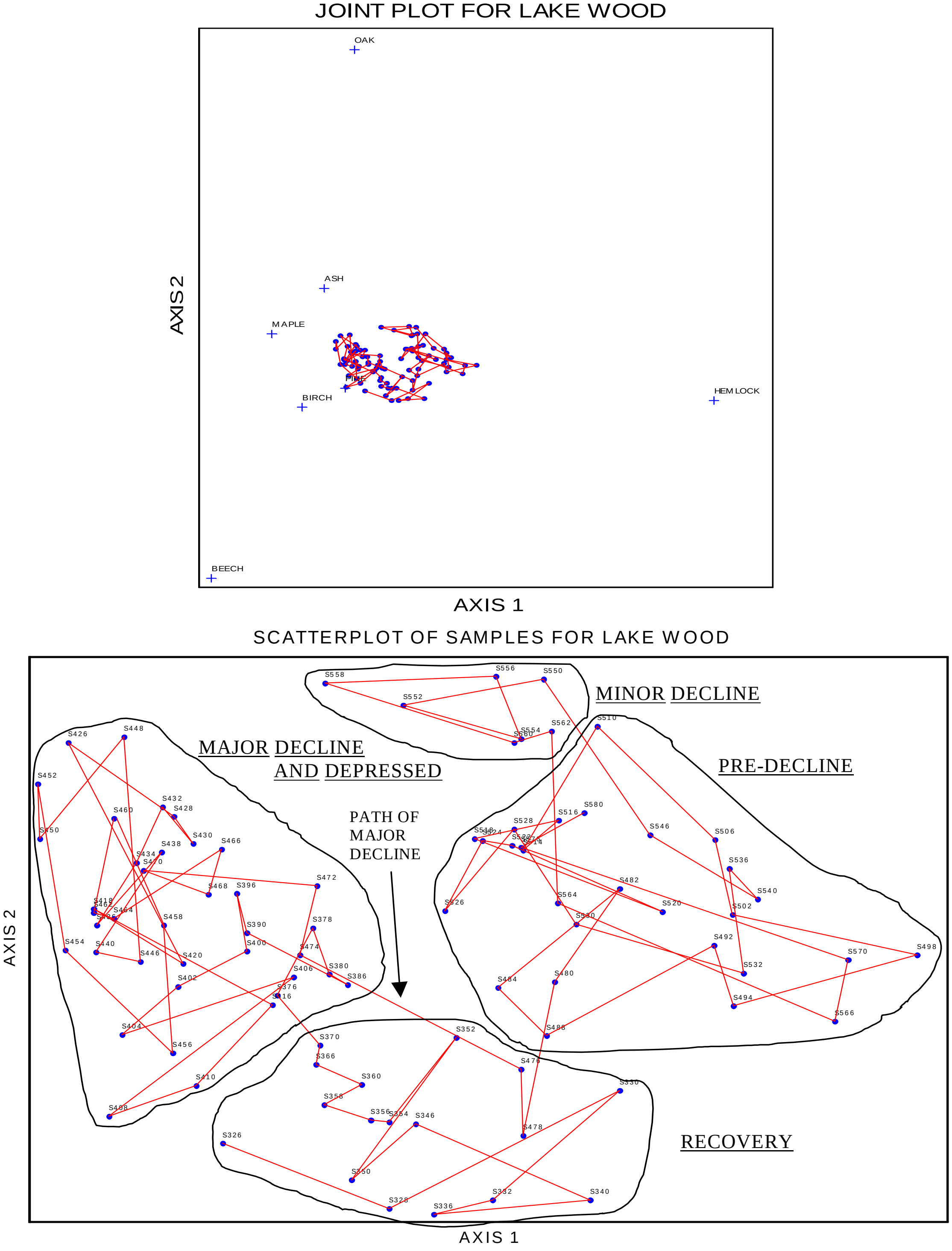


SCATTERPLOT OF SAMPLES FOR THE BOWL



Top joint plot is species data (+) and sample data (●) graphed on first two ordination axes. Red lines are successional vectors connecting adjacent levels. The bottom scatterplot is sample data only to better illustrate successional vectors and includes polygons which encompass groups of samples corresponding with zones on pollen diagrams.

Figure 14: Detrended correspondence analysis for fossil pollen data from Lake Wood.



JOINT PLOT FOR LAKE WOOD

SCATTERPLOT OF SAMPLES FOR LAKE WOOD

Top joint plot is species data (+) and sample data (●) graphed on first two ordination axes. Red lines are successional vectors connecting adjacent levels. The bottom scatterplot is sample data only to better illustrate successional vectors and includes polygons which encompass groups of samples corresponding with zones on pollen diagrams.

CHAPTER 4

DISCUSSION

Fuel Loads and Fire Behavior in Modern Hemlock Stands

Interpreting Fire Behavior Characteristics

The output variables of the fire behavior predictions can appear daunting or even meaningless to those unaccustomed to their use. Some context is required for discussion. Rothermel (1983) contains detailed discussions of concepts only briefly explained below. Fireline intensity, flame length, and rate of spread are the variables most often used to determine what level of personnel and equipment are needed to control a fire. Fireline intensity and flame length are strongly correlated. While fireline intensity is the more precise of the two measurements relative to heat output, flame length is easily observable in the field. Generally, fires with flame length <1.2 m (fireline intensity less than 396 kW/m) can be controlled directly by personnel using hand tools, *i.e.*, hand-constructed control lines should hold the fire. Fires with flame lengths from 1.2 m - 2.4 m (fireline intensities of 396 kW/m - 1729 kW/m) are too intense for direct attack, and heavy equipment such a bulldozers, pumpers, and aerial retardant drops are required for control. Any efforts to control a fire at its spreading front when head fire flame lengths are 2.4 m - 3.3 m (fireline intensity of 1729 kW/m to 3459 kW/m) will probably be ineffective. Flame lengths >3.3 m (fireline intensity >3459 kW/m) represent uncontrollable fires with flames spreading from tree crown to tree crown, spot fires being ignited by burning material long distances ahead of the main fire, and extreme fire behavior including “fire whirls” and “blow-ups”.

Rate of spread is also easily observable and certainly of concern to firefighters, but it is not directly correlated with intensity. A compacted litter fuel bed under a dense canopy may have low intensity and rate of spread, while fire spreading slowly through heavy slash fuels may have high intensity (i.e. long flame lengths). Rates of spread of 0.5 m/min are considered low, 2 m/min - 3 m/min moderate, 10 m/min high, and 40 m/min is considered very high (Scott and Burgan 2005). When rates of spread increase unexpectedly (usually in response to changes in wind speed or to increases in degree of slope on which a fire is burning), fire crews are most vulnerable not only to losing control of the fire, but also to being over-run by the flames.

Most wildland fires spread over the surface of the ground and are propagated primarily by fine fuels. Heavier fuels are ignited by the passing flame front and may burn for a considerable time after the flame front has passed. Fire intensity in heavy fuels is often high, but rates of spread low. Fires spreading in fine fuels may be of low or high intensity, but residence time - the amount of time fire is burning in a given spot - is short. Fires in heavy fuels generally have high total heat output and severity (consumption of organic matter) when fuels are dry. Heat per unit area is useful for assessing fire behavior in heavy fuels, as the variable indicates the total heat output through the duration of the extended residence time associated with heavy fuels. For a sense of scale, note the differences in heat per unit area in the fire behavior predictions (Table 4) between the low-load broadleaf litter fuel model (TL2; 1,639 kJ/m^2) and the moderate-load slash fuel model (SB2; 11,372 kJ/m^2).

Heavy fuels tend to retain higher fuel moistures than finer fuels, thus less of the heavy fuel particles may be available to burn under normal conditions (*i.e.*, a greater proportion of the fuel particle is likely to have a fuel moisture greater than the moisture of extinction). During dry spells or drought conditions, heavy fuels can present an entirely different set of fire control challenges than those of fast-spreading fires in light fuels. As discussed previously, total heat output can be higher and severity greater, but fires in heavy fuels may also burn for days or even weeks generating smoke and possibly firebrands that may start new fires.

Implications of Hemlock Mortality for Fire Behavior

The primary purpose of examining fuels and fire behavior in this study is to determine if high mortality in hemlock stands leads to an increase in fuel loads and potential fire behavior. The affected stand exceeds the unaffected stand in every variable of fuel load and fire spread and intensity analyzed (Tables 3 and 4). If conditions were favorable and a source of ignition present, one could certainly expect more severe fires in a hemlock stand that had experienced extensive die-back or mortality than in a healthy stand. With these results in mind, fire managers would be wise to assess fuel loads and potential fire behavior in adelgid-affected stands to determine if results reported here are applicable to their own situation.

Close examination of predicted fire behavior reveals interesting implications from a fire control perspective. With a flame length of 0.21 m and a rate of spread of 0.23 m/min, fire behavior in the unaffected stand would be well under the upper limit of controllability by hand crews. The affected stand has a higher rate of spread and flame length, although the predicted flame length of 0.91 m is still below the 1.2-m limit for direct attack using hand tools. The 1.5 m/min rate of spread is moderate. Predicted fire behavior in the affected stand does not seem to pose a serious threat in terms of ability to control a surface fire. Fuels in affected stands could cause control problems from extended burning times of the heavy fuels, but the heat per unit area of the affected stand, although more than three times that of the unaffected stand, is only 8240 kJ/m² compared to the heat per unit area of 11,372 kJ/m² for standard fuel model SB2 (a lower intensity slash/blow down fuel model). Under extended drought conditions, with low fuel moistures in even the heaviest fuels, severe burns could produce very high heat per unit area. BehavePlus, however, does not model the outputs of extended burning after a flaming front has passed,

One should note that both the affected and unaffected stands were strongly dominated by hemlock (mostly dead hemlock in the case of the affected stand). The unaffected stand had little understory vegetation and the affected stand presumably had little understory before the adelgid-caused mortality. Stands with less hemlock or mixed hemlock-hardwood stands might have different fire behavior both before and after a hemlock decline. A denser understory, the presence of more fire-prone hardwoods (*e.g.*, oak), the presence of less fire-prone hardwoods (*e.g.*, sugar maple), and different patterns in seasonal availability of fuels may affect the incidence of fire before a hemlock decline and thus lead to a different change in fire than that implied above for stands strongly dominated by hemlock. Both the affected and unaffected stands sampled are second-growth. Old growth hemlock stands would have more dead, down wood that may contribute to increased fire intensity and burn severity (under drought conditions).

Following a hemlock mortality episode (due to insect/disease or blow-down) there would exist temporal variability in the abundance of available (to burn) fuels in different size classes. Fine fuels (needles, twigs, small branches) would fall from dead trees to the surface and decay relatively quickly (within a few years) compared to heavy fuels (large branches, boles) which would fall some years later and take substantially longer – perhaps decades - to decompose (Woodall and Nagel 2007). While the overall fine fuel loading at the affected stand I sampled was about twice that of the unaffected stand (mostly due to abundant birch litter in the affected stand), the heavy fuel loading was three to seven times greater in the affected stand. The affected stand was sampled after most of the fine fuels from hemlock mortality had decayed. Fire spread and intensity is primarily driven by fine surface fuels. One can reasonably speculate that if the affected stand had been sampled at the peak of the fine fuel pulse, predicted intensity and rate of spread would be greater for the affected stand than that predicted by the data collected.

Relationship of Hemlock Pollen to Charcoal and Pollen of Other Taxa

The major hemlock decline is clearly reflected in changes in pollen percentages at The Bowl and Lake Wood on the central Maine coast, and at Hawley Bog and Larkum Pond in western Massachusetts. Two or perhaps three declines are evident in the Round Pond diagram, each of which is less pronounced than at the other sites. The hemlock decline beginning around 240 cm is assumed to represent the major decline (see RESULTS). Hemlock percentages decline 84% over 30 centimeters from a high of 16.3% at 245 cm to a low of 2.6% at 215 cm; a clear decline, but over a wide range of levels and with the lowest pre-decline hemlock percentage of any of the five sites. A possible explanation for the subtlety of the decline at Round Pond is that the watershed lies in a glacial outwash feature with sandy soils that have long been dominated by more drought-tolerant taxa, particularly pine and oak. Hemlock was never locally abundant there. Additionally, the Round Pond site was chosen specifically because fire is presumed to have been more common than at other study sites. Between the predominance of fire and droughty soils, one would not expect hemlock to have ever been a dominant component of the vegetation.

Although charcoal:pollen ratios do not exceed 450 μm^2/gn at Round Pond and do not exceed 175 μm^2/gn at any of the other four sites, all sites have increases in ratios during the major decline or the depressed period. As expected, higher overall ratios occur at Round Pond (in the Connecticut Valley with outwash soils), lower ratios at Hawley Bog (a high elevation, northern hardwoods environment), and intermediate ratios at The Bowl, Lake Wood, and Larkum Pond.

The Bowl has a clear series of charcoal peaks at the onset of and during the major decline which largely subside once hemlock levels more or less stabilize at lower percentages during the depressed hemlock period. The Bowl also exhibits a minor decline starting at about 274 cm before the major decline which starts at 255 cm. There is a large charcoal peak corresponding with the lowest hemlock sample during this minor decline.

Similarly, the Lake Wood diagram has a large peak of charcoal at the onset of the major decline (around 475-480 cm) followed by another large peak corresponding with the end of the major hemlock decline (around 460 cm). Additionally, the Lake Wood diagram indicates a large decrease in charcoal starting at around 515 cm which is accompanied by a rise in hemlock pollen, further strengthening the hemlock-fire connection. Given the fire-sensitivity of young hemlock, it is possible that if there is a cause and effect relationship in this instance, it may be that the decrease in fire allowed hemlock to increase in abundance. The data for the two Maine sites clearly indicate increased fire activity associated with hemlock declines, and were the original inspiration to investigate the regional link between hemlock decline and fire regime dynamics.

At Hawley Bog, there are charcoal peaks during the depressed hemlock period, but none are apparent during the major decline. There are also charcoal peaks before the decline of greater magnitude than those following the decline. Hawley Bog sediments contain very low levels of charcoal – values so low that they would not be interpreted as evidence of locally occurring fire at most sites.

While it is certainly possible that there were increased post-decline fuel loads around Hawley Bog that simply never ignited before they decayed, another possible explanation for the lack of charcoal peaks and the low charcoal levels in general lies in the mechanism for charcoal transport. Hawley Bog is a true bog with a deep, wide peat mat inhibiting influx of sediments via surface runoff. Assuming the water body existed in a bog state during the mid-Holocene, only air-borne charcoal would reach the small pond in the middle of the bog (from which sediments were raised). The date of onset of the development of the peat mat at Hawley Bog is speculative, as local climate conditions in addition to topography, hydrology, and time of glacial retreat all contribute to bog formation. A sediment core or cores through the peat mat (rather than from below open water) and radiocarbon dating of the core would provide the most confident dates for the initiation of peat mat development. A study conducted on bog development in Sweden (Almquist-Jacobson and Foster 1995), lends some credibility to the assumption that the peat mat existed at Hawley Bog during the time of the major hemlock decline. The study concluded that raised bog formation began in the Bergslagen region of Sweden at 4,000 to 5,000 ^{14}C yr BP. Note that the Bergslagen region lies at 60°N latitude and Hawley Bog lies at 42°N where average temperatures are presumably warmer (elevations at both sites are under 600 m). Given that bog growth is limited by low temperatures (Almquist-Jacobson and Foster 1995), the Hawley Bog peat mat may have been initiated, and possibly well-developed, by the time of the hemlock decline (4750 ^{14}C yr BP). Additional support for pre-hemlock decline bog formation can be found in Anderson *et al*. (2003), who found shrub-derived peat formation began in three bogs in central New England as early as 8,500 to 9,600 calendar years BP.

Hawley Bog's low charcoal levels also mean that even a small increase in charcoal abundance could represent an increase in fire activity at the regional scale, because the relative increase may be large. For example, there is a charcoal peak at 239 cm of 29 μm^2/grain with surrounding levels at about 14 μm^2/grain: an absolute increase of only 15 units in a context where 1,000 units is high, but a relative increase of almost 50%. Additionally, with surface-borne charcoal filtered from runoff before it could reach the center of the bog, airborne charcoal, representing regional fires (Clark and Patterson 1997), would be overweighted relative to charcoal produced by local fires.

The two or three peaks in charcoal at the end of the decline may reflect a change in fire regime during the depressed period related more to changes in vegetation than to abundant dead hemlock. Following the hemlock decline, oak percentages rise from around 12% to just over 15% (a 25% relative increase). Oak fuels are generally more flammable than hemlock (and associated northern hardwood) fuels, so possible post-decline peaks in charcoal may reflect increased fire activity in response to increased dominance of oak.

Although the decline itself is more subtle at Round Pond - probably due to less hemlock present in the watershed than at the other sites - charcoal:pollen ratios demonstrate clear and pronounced peaks during the hemlock decline. One peak is more than three times larger than the background charcoal levels and is not exceeded at any other point in the data set. Round Pond is surrounded by a peat mat like Hawley Bog, although the Round Pond peat mat is only a few meters wide while the Hawley Bog peat mat is up to 200 meters wide. Also, Hawley Bog has a much larger deposition basin than Round Pond (26 ha versus 2 ha). In addition to the surrounding bog mat, Round Pond has no inlets or outlets, and the surrounding landscape is flat. Like Hawley Bog (but perhaps to a lesser extent), charcoal transport to Round Pond is primarily aeolian. This pattern of a subtle hemlock decline with pronounced charcoal peak makes sense given the low hemlock occurrence but high fire occurrence expected on sandy outwash soils.

The hemlock decline at Larkum Pond is clear and pronounced. There are peaks in charcoal abundance, but they do not seem to be specifically related to the major hemlock decline, as they occur before, during and after the major decline. Larkum Pond is unique among the study sites in that pollen assemblages before the decline are strongly dominated by hemlock at around 40%. None of the other sites exceed 25%. Hemlock is also prevalent around the pond today. Larkum Pond was probably intermediate between Round Pond and Hawley Bog in prehistoric fire occurrence. This assumption is based on differences in climate, elevation, soils, and ignition sources among the three sites. Larkum Pond is at a higher elevation and has less well-drained soils than Round Pond contributing to moister conditions. The upland probably supported a lower aboriginal population (leading to fewer ignitions) than Round Pond in the Connecticut Valley

(Patterson and Backman 1988). Hawley Bog is at a higher elevation and more isolated from human ignition sources than either Round or Larkum Ponds, so human ignitions were probably less common there.

In summary, there are three sites (The Bowl, Lake Wood, and Round Pond) where increased fire activity is clearly linked to the major hemlock decline and two sites (Hawley Bog and Larkum Pond) where there appears to be no link or an ambiguous relationship between fire occurrence and declining hemlock abundance. The two sites with no apparent increase in fire activity at the time of the major decline have very clear hemlock declines with one of them (Larkum Pond) having the most pronounced decline of any of the sites. Of the three sites with clear increases in fire activity, The Bowl and Lake Wood have a distinct hemlock decline while Round Pond has a subtle decline. The sites with clear links between fire increase and hemlock decline are either coastal (The Bowl and Lake Wood) or occur in a fire-prone environment (Round Pond). The two sites without fire increases specifically associated with the hemlock decline are on more mesic, high-elevation, inland sites with presumably fewer ignitions.

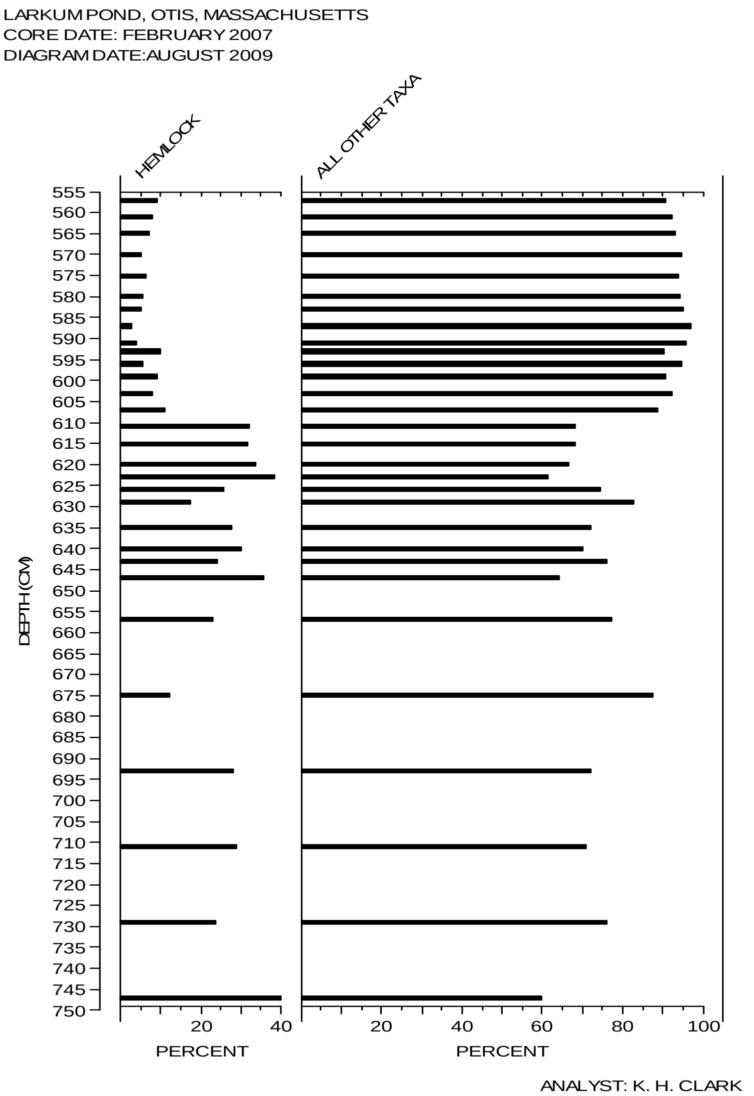
While the pollen diagrams fail to provide a clear and universal answer to the principal question of this study – Was there a change in the fire regime associated with the mid-Holocene hemlock decline? – they do suggest an interaction between hemlock decline and fire regimes at some sites. An increase in fire specifically due to the decline seems more related to an active fire regime in general and the relative abundance of hemlock before the decline, rather than to the magnitude of the decline itself. The magnitude of the hemlock decline seems most related to the pre-decline dominance of hemlock.

The Nature of Relative Data

After the onset of the major decline, one would expect other taxa in the data set to increase for two reasons. First, when hemlock declines, other taxa should increase for ecological reasons (*i.e.,* due to community composition changes). Second, the data are presented on a relative basis; the pollen of each taxon is measured as a percentage of the sum of all pollen for that sample. If one pollen type drops substantially, the percentages of other taxa increase solely because of the relative change in the composition of the data set. To illustrate this concept graphically, a pollen diagram was developed from the Larkum Pond data (Figure 15) in which hemlock pollen percentages are presented alongside all other taxa merged into one group. Note the corresponding rise in all other taxa on the diagram when hemlock declines. Larkum Pond was chosen for this example because it has the most precipitous and abrupt hemlock decline, thus illustrating the relative change issue to the greatest degree among all the data. The non-hemlock taxa average 72% before the hemlock decline and 93% after the decline, i.e., the 21 point drop in hemlock has been reflected as a 21 point rise in all other taxa strictly because of the relative nature of the data. Also note that the change is essentially instantaneous (between 606 cm and 610 cm), and is thus too fast to represent increased pollen production due to response of other taxa. The smaller rise in subsequent samples while hemlock does not change much more likely represents a biological response of successional species.

The challenge in interpreting the ecological significance of changes in pollen abundance with the decline of one dominant type is to determine the extent to which a change in pollen of a given taxon is due to the relative or “across-the-board” change versus the ecological change. Patterson (2005) examines this issue in detail. The surest

Figure 15: Hemlock pollen versus pollen of all other taxa combined at Larkum Pond.



manner to overcome the flaw of data relativity in percentage counts is to calculate pollen influx rates which provide estimates of the absolute abundance of pollen grains. Unfortunately, pollen influx rates require accurate dating of the sediments provided by isotope dating, which is prohibitively expensive in most cases (Patterson 2005).

Fortunately, the sheer number of taxa largely masks the relative changes in pollen percentages. For example, the Larkum Pond non-hemlock taxa change from 72% before the hemlock decline to 93% post-decline: an approximately 23% relative change. (*n.b.* Do not be confused by the change in absolute percentage points which is 21 versus the relative change from 93 to 72 which is a 23% change; the closeness of the two numbers is coincidental, and it is the "percent change between the two percentages" that is important to this argument.) There are 45 non-hemlock taxa represented in the Larkum Pond data set (taxa with very low numbers that are not stratigraphic markers or have other ecological significance are present in the calculations but are not shown on the diagrams to conserve space). A 23% change spread out over 45 taxa is 0.5% change per taxon due to relative change only. One can take a highly conservative view by eliminating the 38 taxa which have at least one zero in the dataset, leaving 7 non-zero, non-hemlock taxa. A 23% total change spread out over 7 taxa (*i.e.*, 23 divided by 7) is 3.3% change per taxon. Recall this is relative change, not increase in percentage points. For example, a taxon at 2% before the decline might rise to 2.07% after the decline while a taxon at 20% pre-decline would rise to 20.7% after the decline as a result of relative change only. Therefore, one can largely ignore the relative increases and assume any changes of more than one or two percentage points are, in fact, a reflection of real changes in composition of the community or normal random fluctuations in the pollen data rather than changes due to the relative nature of the data.

To illustrate this point further, we can remove an abundant taxon completely from the data and re-analyze the data. If the relative changes in percentages of other taxa are not large and if the pattern of the relative abundances remains stable, we can conclude that the across-the-board increases are not ecologically significant and can be ignored in the interpretation. This prediction is, in fact, exactly what is seen when the hemlock data are removed and the Hawley Bog dataset re-analyzed (Table 7). Every taxa at every sample increases, but the degree of increase is small (rarely exceeding 2%) and the patterns of change within each taxon across the samples are unaltered. By choosing hemlock as the omitted taxon - the taxon which experiences the greatest change in all five diagrams - one can further examine the effects in the context of large relative abundance changes in one taxon. Again, the Hawley Bog dataset with hemlock omitted experiences no alteration of overall pollen trends within each taxon, and the only difference before and after hemlock is removed from the dataset is the magnitude of the changes. Before

Table 7: Comparison of Hawley Bog Data with Hemlock Included and Excluded from Dataset.

depth (cm)	percent of total pollen by taxon observed in hemlock-included dataset (+) and hemlock-excluded dataset (-)											
	pine		birch		oak		sugar maple		hickory		beech	
	+	-	+	-	+	-	+	-	+	-	+	-
210	8.7	9.3	23.7	25.3	21.2	22.5	2.9	3.0	2.0	2.1	22.6	24.0
220	6.8	7.2	20.8	22.0	20.8	22.0	5.6	6.0	1.8	1.9	21.7	23.0
230	7.1	7.5	25.5	27.0	20.3	21.5	2.9	3.1	0.3	0.3	21.3	22.5
231	5.4	5.6	28.0	29.2	18.8	19.6	4.5	4.7	1.5	1.6	25.0	26.1
232	6.3	6.7	27.0	28.3	16.2	17.0	4.4	4.7	1.0	1.0	27.3	28.7
233	6.8	7.3	30.2	32.4	15.1	16.2	3.1	3.4	2.5	2.7	19.2	20.6
234	8.1	8.5	24.4	25.7	12.7	13.3	5.0	5.3	0.9	0.9	24.4	25.7
235	9.5	10.1	25.2	26.8	15.4	16.4	2.3	2.4	2.3	2.4	27.2	28.9
236	5.1	5.2	28.0	28.9	14.6	15.1	2.7	2.8	1.8	1.8	31.3	32.3
237	6.0	6.4	26.4	27.8	14.3	15.1	5.2	5.5	1.1	1.2	28.0	29.6
238	5.0	5.2	28.0	29.0	13.3	13.8	4.6	4.7	1.3	1.3	30.9	32.0
239	6.5	7.0	27.9	30.3	10.9	11.8	5.7	6.2	0.0	0.0	24.3	26.3
240	5.5	6.0	29.0	31.6	14.3	15.6	2.9	3.2	1.3	1.4	22.8	24.8
241	7.3	7.8	28.4	30.4	15.2	16.3	3.8	4.1	1.2	1.3	24.6	26.3
242	3.5	3.9	30.9	34.4	14.1	15.7	4.0	4.5	1.3	1.5	22.2	24.7
243	3.4	3.7	33.4	36.2	13.7	14.8	3.1	3.3	1.7	1.8	25.6	27.7
244	5.0	5.6	27.9	31.7	15.7	17.9	3.5	4.0	1.6	1.8	22.2	25.1
245	2.9	3.4	30.4	35.2	13.8	16.0	4.4	5.1	0.8	1.0	20.5	23.7
246	3.6	4.4	31.5	38.5	13.8	16.9	2.4	3.0	1.2	1.5	19.6	24.0
247	3.9	4.7	29.5	36.1	11.5	14.0	1.2	1.5	2.2	2.7	23.3	28.5
248	3.8	4.5	30.3	36.2	12.9	15.4	2.5	3.0	1.4	1.7	22.2	26.5
249	3.0	3.6	25.0	30.8	13.2	16.3	2.8	3.4	0.7	0.9	25.7	31.7
250	5.6	7.1	21.8	27.4	14.2	17.9	3.4	4.3	1.0	1.2	21.6	27.1
260	4.0	4.8	27.3	32.7	15.9	19.0	3.3	3.9	3.3	3.9	16.8	20.1
270	5.5	7.4	22.8	30.6	12.9	17.3	1.8	2.4	3.0	4.0	18.3	24.5
280	2.4	3.3	27.1	37.7	14.5	20.2	2.4	3.3	2.7	3.8	14.9	20.8
290	5.7	7.7	22.3	30.2	15.3	20.7	0.9	1.2	0.9	1.2	17.5	23.7
300	4.8	6.6	16.6	22.8	17.3	23.9	2.9	6.6	0.0	0.0	16.2	22.3

n.b.: only six taxa are shown due to space limitations, but analysis was conducted on all taxa in dataset the decline, when hemlock represents around 20% to 25% of the pollen, each taxon rises 1% to 2% from the hemlock-included to the hemlock-excluded analysis. Post-decline, each taxon rises only 0.2 – 1.0 %, because hemlock represents only approximately 10% of the pollen. If a single taxon very strongly dominated the pollen spectra (e.g., $\geq$60%) and then declined precipitously, the relative change in the other taxa would be more dramatic. For purposes of this study, however, in which hemlock does not exceed 45%, the post-decline relative increases in other taxa are not important.

Response of Other Vegetation to Hemlock Decline

In modern hemlock stands suffering heavy adelgid-caused mortality, there are increased abundances of early successional species, particularly birch. Orwig (2002) found that black birch (*Betula lenta*) rapidly dominated adelgid-affected stands in Connecticut. Adelgid has been active in southern New England only since about 1985 (Orwig *et al.* 2002), so data regarding long-term changes in forest composition are not yet available. Jenkins *et al.* (2000) predict that American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*) will come to dominate their study site in northwestern Connecticut, and note that forest development after adelgid infestation will depend on the composition of the forest community when the adelgid arrives. Heard and Valente (2009) used mid-Holocene hemlock decline data to forecast response of other vegetation following adelgid-caused hemlock mortality at modern sites. They predict that maple, birch, beech, and oak are the genera most likely to respond positively to declining hemlock abundances.

Numerous studies of the mid-Holocene hemlock decline find that hemlock is followed first by an increase in birch and then an increase in hemlock competitors (northern hardwood species in northern New England, oaks in southern New England). Davis *et al.* (1985) postulate that increased light on the forest floor permits germination of birch seedlings. In New Hampshire, they document an increase in birch pollen as hemlock pollen declined. Other early successional species which are poorly represented by the pollen record such as black cherry (*Prunus serotina*) may have also increased in response to the decline (Davis *et al.* 1985). Allison *et al*. (1986) summarize results from several New England and midwestern U.S. sites where birch increased in sediments deposited immediately after the decline. After the birch increase, maple and beech pollen increased in northern New Hampshire, oak and white pine increased in southern New Hampshire, and white pine and other conifers increased in northern Michigan. Foster and Zebryk (1993) found pine and oak increased after the decline in central Massachusetts. Fuller (1998) found birch, beech, sugar maple, elm, oak and white pine increased following the decline at two southern Ontario study sites. In Quebec, white pine dominated pollen assemblages following the decline (Bhiry and Filion 1996).

Like modern hemlock stands and previously studied prehistoric populations, birch pollen generally increases during or just after the hemlock decline at sites examined for this study. Although gray birch pollen can be identified to species (by grain size), no attempt was made to differentiate among the four species of birch that are common to the region surrounding the five sites of this study. Based on the ecological context, however, one may assume that the early successional birch species characteristic of the region - gray, paper or black birch for western Massachusetts and paper or gray birch for Maine - are the species experiencing post-decline increases in the paleoecological record. Birch demonstrates a subtle, consistently short-lived (usually not more than one or two samples) increase of 5% to 10% followed by a comparable decrease towards the end of the decline at each of the five sites, although other species may increase or decrease at the same time as birch depending on the site. An exception with respect to the magnitude of the change in birch is Lake Wood where birch increases over 10% and remains elevated until hemlock begins to recover. With an increase of more than 2%, change exclusively due to relative percentage increases can be ruled out in these cases.

After the birch increase, four sites - The Bowl, Lake Wood, Hawley Bog, and Larkum Pond - demonstrate a rapid increase in either beech or oak followed by a prolonged increase in other taxa. The Bowl and Lake Wood have rapid increases in oak immediately after birch increases, followed by a prolonged increase in beech. Larkum Pond and Hawley Bog have relatively short-lived beech increases (contemporaneous with the birch increase in the case of Larkum), then a long, steady increase in oak. Round Pond is an exception with a short-lived beech increase, but no clear oak increase. This may be due to the fact that oak was already dominant at Round Pond before the decline and demonstrates large fluctuations in percentages (possibly due to more coarsely textured, droughty soils leading to a more active fire regime), so a subtle increase may be masked by other factors. Consistently - across all five sites - pine increases slightly (*e.g.*, by 2%-5%) during or after the hemlock decline. These trends are consistent with the original postulate that hemlock was quickly replaced by pioneering tree species such as birch, and stands succeeded to northern hardwoods, pine, or other mature hemlock competitors until hemlock recovered centuries later.

The pollen diagrams indicate too large a gap in time for the successional peaks in oak and beech to be explained by delayed pollen production. For example, birch increases contemporaneously with the onset of the hemlock decline at Hawley Bog (at about 247 cm), a beech increase begins at approximately 180 years after the hemlock decline (at 238 cm), and an oak increase begins approximately 280 years after the decline (at 233 cm). Beech and oak generally begin producing substantial amounts of pollen at 30 to 50 years of age (Burns and Honkala 1990), therefore increases in beech and oak strictly due to delayed pollen production would occur deeper in the diagram closer to the hemlock decline.

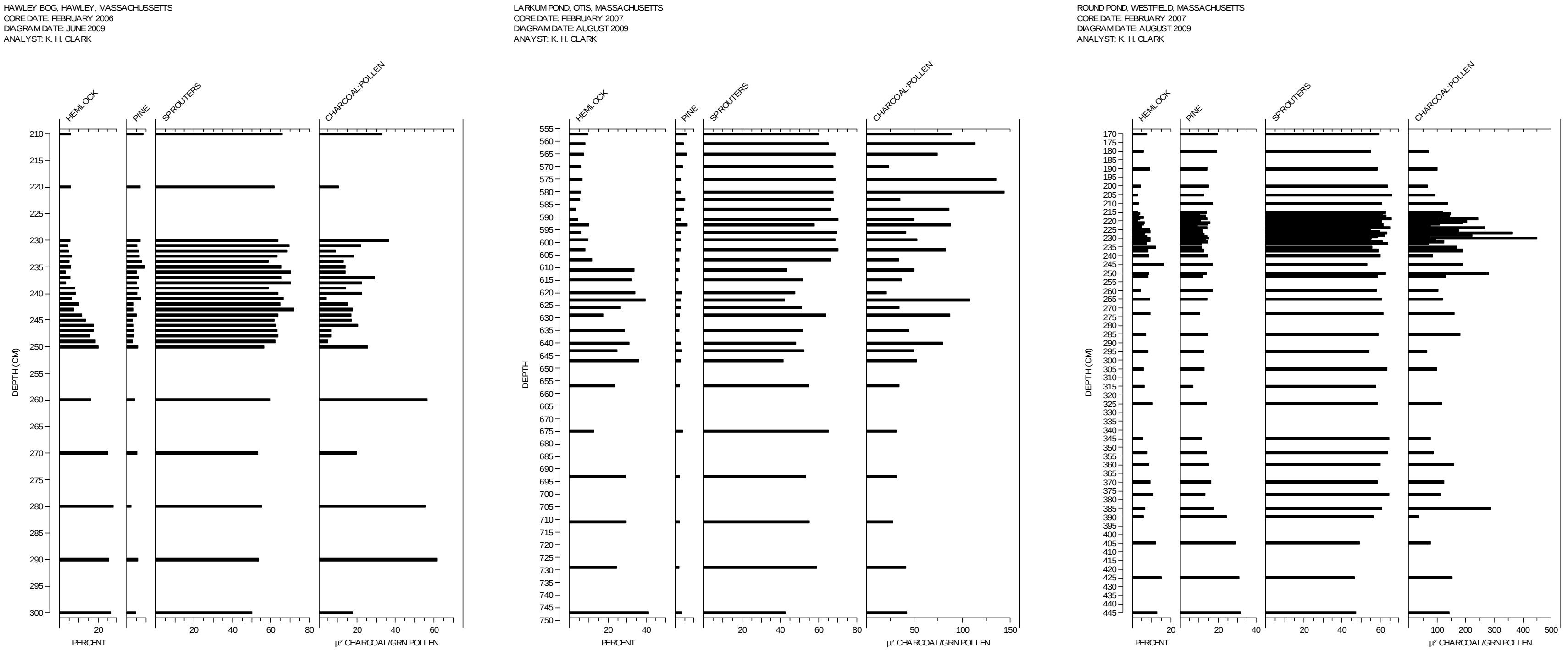
Disturbance Indicated by Vegetation Trends

Past occurrences of ecological disturbances such as fire may be inferred indirectly from vegetational changes detected by fossil pollen analysis. Swain (1973) suggests that increased fire occurrence may be reflected in pollen diagrams by decreases in the abundance of species which reproduce only from seed, especially conifers, and/or by increases in species that reproduce vegetatively primarily from stump sprouts or root suckers. Many herbaceous species respond to fire with dramatic increases (or decreases) in flowering, but most forest herbs are insect-pollinated and thus not well-represented in the pollen rain (Swain 1973). Tree species, however, which reproduce vegetatively after fire, may flower prolifically in a few to several decades and thus be detected by pollen analysis of sediments.

Aside from hemlock, pine is the most abundant conifer at all five sites in this study, but does not vary consistently following the major hemlock decline across all sites. Hawley Bog and Larkum Pond have no discernable drops in pine related to either the hemlock decline or to fire following the onset of the decline (Figures 5 and 6). Both sites have low pre-historic pine pollen abundances, rarely exceeding 10% of the pollen profile suggesting pine is more important regionally than locally. Pine is more important locally at Round Pond, The Bowl, and Lake Wood (15% to 40% of the pollen spectra). Small, short-lived declines (*i.e.*, generally <5% lasting one or two samples) in pine occur at Round Pond and The Bowl (Figures 7 and 8). These declines correspond with the hemlock decline and peaks in charcoal. At Lake Wood (Figure 9) pine drops 15% as charcoal increases at the onset of the hemlock decline. The relative dominance of pine seems to determine its usefulness in reflecting ecological disturbances such as fire. Where pine is abundant, a short-term decrease in its abundance may indicate an increase in fire activity (Swain 1973).

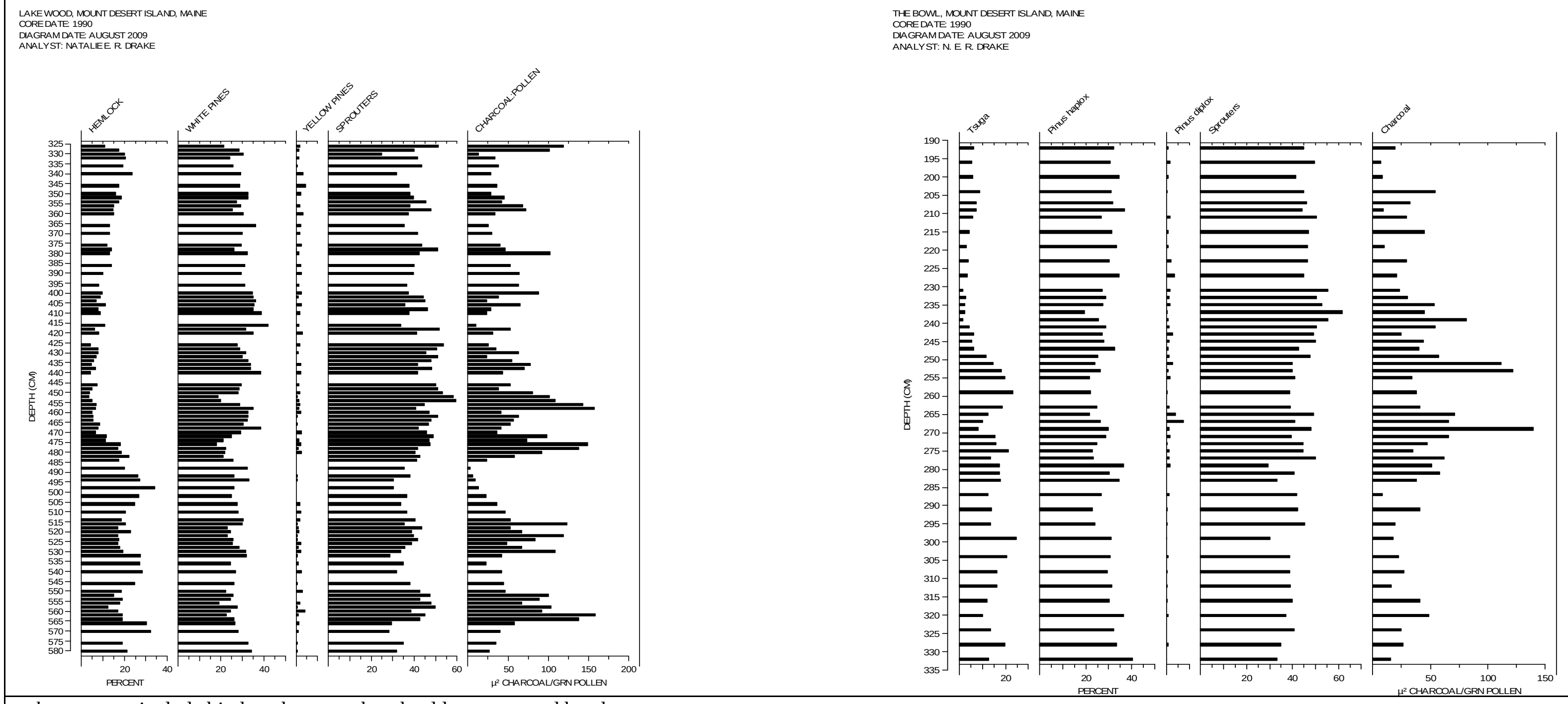
There are several taxa which sprout or spread rhizomatously after fire and occur in the pollen profile for all five sites. Following the example of Swain (1973), data for birch, oak, aspen (*Populus* spp.), beech, alder (*Alnus* spp.), grasses (Poaceae), and bracken fern (*Pteridium*) were lumped together as “sprouters”. Pollen sums were not altered; only the way in which some taxa, *i.e.*, those that sprout in response to disturbance, are presented. Birch, oak, and beech were well-represented at all five sites; whereas aspen, alder, grasses, and bracken were less abundant but still present. Pollen data for each site were re-analyzed with the seven sprouter species omitted individually but shown in an aggregate manner as “sprouters” (Figure 16) in order to highlight trends not evident from changes in individual species. At Hawley Bog (Figure 16) three peaks of sprouters of at least 5% (absolute increase rather than relative, in this case) above background levels occur following the hemlock decline. All sprouter peaks correspond to peaks in charcoal. The other modified pollen diagrams (Figure 16) demonstrate a similar

Figure 16: Fossil pollen and charcoal diagrams showing sprouters.



n.b. sprouters include birch, oak, aspen, beech, alder, grass, and bracken

Figure 16: Fossil pollen and charcoal diagrams showing sprouters (continued).



n.b. sprouters include birch, oak, aspen, beech, alder, grass, and bracken pattern: a series of peaks (5% to 10% increase in sprouters) during the hemlock decline, often with corresponding charcoal peaks. Although subtle, increases in sprouters seem to support other data (charcoal peaks, conifer decreases) suggesting that there were a series of fires following the hemlock decline at most sites.

Visualizing Pollen Trends with Multivariate Analysis

Overall, the DCA scatterplots (Figures 10 through 14) effectively mirror the trends identified in the fossil pollen diagrams (Figures 5 through 9), and illuminate additional patterns relevant to hemlock trends.

Hawley Bog

Pre-decline samples have strong hemlock dominance and lower oak dominance than post-decline (Figure 10). As the decline progresses, samples migrate left along axis 1 and down along axis 2 reflecting decreasing hemlock and increasing birch and beech. An increase in maple in these samples also contributes to lower axis 1 scores. During the period of depressed hemlock percentages, samples move farther to the left on axis 1 as maple, beech, and pine increase. Ash peaks and birch decreases at the end of the successional vector causing an upwards shift along axis 2 in the depressed period group of samples.

Larkum Pond

The widespread (along axis 1) pre-decline group reflects the fluctuation of hemlock among high percentages early in the data (Figure 11). Hemlock ordinating alone and far to the right along the first axis reflects the great importance of hemlock at the site before the major decline. A minor decline is evident prior to the major decline as two samples migrate left on axis 1 (hemlock decrease) and down on axis 2 (birch increase).

The major decline is precipitous as demonstrated by the single sample in the decline group farther to the left on axis 1. During the depressed period, the position of the group far to the left on axis 1 and low on axis 2 reflects low hemlock percentages and increasing beech percentages. Movement of samples higher on axis 2 and slightly to the left on axis 1 at the end of the successional vector reflects an oak increase and possible initiation of hemlock recovery.

Round Pond

The Round Pond scatterplot reflects the ambiguous nature of the disturbance history for that site (Figure 12). There are two pre-decline samples that ordinate far to the right on axis 1 due to very high (relative to the rest of the dataset) hemlock percentages. A minor decline group ordinates farther to the left on axis 1 (lower hemlock) and low on axis 2 (oak increase). From the end of the minor decline, the data become rather ambiguous with the depressed hemlock period and some pre-decline samples ordinating in the same area. The successional vector clearly leaves this area into a major hemlock decline group high on axis 2 (higher maple, beech, and ash) and far to the left on axis 1 (low hemlock). The vector then crosses back into the web-like area in the center with the depressed hemlock period samples. Either the depressed period and pre-decline samples are actually similar in vegetation or a combination of variables, some driving the pre-decline samples, some driving the depressed period samples, are causing the two groups to ordinate similarly. Outlying samples from this group lying low on axis 2 are driven by oak peaks while an outlying sample far to the right on axis 1 is from a hemlock peak. Movement to the right on axis 1 of a small group of samples at the end of the successional vector may indicate a recovery period has begun.

The Bowl

In contrast to Round Pond, The Bowl scatterplot is clear (Figure 13). Note that with the exception of the minor decline, successional vectors cross only once from one group of samples to another. For the minor decline, one vector crosses into the decline and one back into the pre-decline group demonstrating the chronology of this minor decline as nested within the pre-decline period. The pre-decline group is far to the right on axis 1 (higher hemlock), while the minor decline lies slightly to the left of it indicating lower hemlock abundance. The major hemlock decline ordinates abruptly on this scatterplot manifesting as one sample (249 cm) between the pre-decline and depressed period groups. Far to the left on axis 1 due to low hemlock percentages, the depressed group ordinates widely along axis 2 reflecting periods of higher oak (higher on axis 2) and periods of higher beech (lower on axis 2). A recovery group is evident as the samples move slightly to the right along axis 1 (higher hemlock, increasing maple) and farther down on axis 2 (increasing beech and maple).

Lake Wood

Lake Wood has the largest number of samples and the most precise overall sampling resolution. The relatively large fluctuations (compared to the other scatterplots) from the high sampling resolution and general noise of the scatterplot make interpretation more challenging, but the general trends are still apparent (Figure 14). To the right on axis 1 is the pre-decline group with a minor decline group emerging to its left (less hemlock) and a little higher on axis 2 (increased oak). The beginning of the decline ordinates within the recovery period group as hemlock percentages fall; note the successional vector leads left along axis 1 but is pulled down into the recovery group’s area by two samples with low beech. Once the vector reaches the depressed period group, the major decline continues for a few samples until hemlock levels become quite low (left on axis 1). During the depressed period, maple, birch, ash, and oak rise as indicated by the depressed group's extension far up on axis 2. As hemlock moves into the a recovery period, samples move back to the right on axis 1. The recovery is accompanied by an increase in beech reflected by samples moving down on axis 2.

Insights from the Data to Cause of the Prehistoric Hemlock Decline

Collection and analysis of high resolution pollen data for the time spanning the mid-Holocene hemlock decline allows examination of associated questions. One of the most controversial is the cause of the decline itself. Hypotheses center on either climate change or a biological agent (pest, disease, or both), and arguments have been made in favor of each.

Margaret Davis and her associates were the first to argue in favor of a biotic cause for the decline (Davis 1981, Davis *et al.* 1985, Allison *et al.* 1986). Davis and others have developed strong indirect evidence for a pest or pathogen: the decline is range-wide, abrupt, synchronous, and no other species apparently are affected. Bhiry and Filion (1996) provided some direct evidence of an insect pathogen as the cause of the decline by documenting abundant chewed hemlock needles and insect part macrofossils in sediments associated with the time period of the decline. Lennox *et al.* (2010) suggest that a biotic cause was more likely at a site they studied in Nova Scotia simply because they saw no evidence in their data to suggest a climatic cause.

Alternatively, Filion and Quinty (1993) examined growth-rings of fossilized trees and concluded there was no physical evidence of insect pest or fungal disease, and note that the decline is closely associated with regional climate change. Haas and McAndrews (2000) suggest a climate-related cause for the decline, specifically summer drought. Shuman *et al.* (2001) found both palynological and sedimentary evidence for a warmer, drier climate in relation to the hemlock decline and suggest climate change was at least a contributing factor to the decline.

Foster *et al.* (2006) recently advocated the climate-change view based on a synthesis of fossil pollen data and physical evidence regarding climate (indicators of drought and low water levels) from selected southern New England sites. Primary support for their argument is that, for the 17 sites they examined, both hemlock and oak declined synchronously; hemlock at inland sites and oak at coastal sites, and that, coupled with sedimentary data, this indicates a drier, warmer period synchronous with the hemlock decline.

The data from this study do not support Foster *et al.*'s suggestion that oak declined synchronously with hemlock. Oak does not decline with hemlock at any of the five sites, and, in fact demonstrates brief increases in relation to the hemlock decline at the coastal sites (The Bowl and Lake Wood) and at Round Pond, and a gradual sustained increase following the decline at Hawley Bog and Larkum Pond. Furthermore, one would expect northern hardwoods (sugar maple, birch) to decrease if the climate became warmer and/or drier. Sugar maple occurs at low levels at all five sites, but demonstrates no sustained decreases synchronous with the hemlock decline. Birch is abundant at all five sites, has no sustained decreases, and actually has brief <u>increases</u> during or following the decline at all five sites.

Further consideration to the climate-change hypothesis might involve the timing of species declines and the resolution at which data are reported. If the hemlock decline were climate-driven, one would expect declines in other taxa to be synchronous with the hemlock decline. The cores from all five sites in this study have been sampled (during the period spanning the major hemlock decline) at an unusually high level of resolution (1 to 5 cm) for a study of the hemlock decline, yielding samples at approximately 20 to 40 year intervals. At this resolution, the major hemlock decline took place over as few as 50 years at Larkum Pond (Figure 6) and as much as 200 years at Hawley Bog (Figure 5). Small, short-lived increases in the pollen of other taxa took place during or after the decline. No synchronous, sustained increase or decrease in pollen of other taxa is seen. Although Foster *et al.* (2006) do not report sample depths, they admit "our stratigraphies are not tightly constrained chronologically" (p. 2965), and note that the hemlock decline and oak decline occur within ≈500 years. This low resolution could easily mask the fact that the oak and hemlock declines did not occur synchronously, but rather that one may have preceded the other by up to a few centuries.

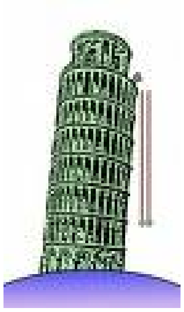
To consider the broader geographic range of hemlock, one can examine the Pollen Viewer tool (http://www.ncdc.noaa.gov/paleo/pollen/viewer/webviewer.html based upon Williams *et al.* 2004) which depicts (based on many studies) fluctuations in abundances of species associated with pollen types for various taxa across North America. The major hemlock decline occurs between the 6,000 ^{14}C yr BP and 5,000 ^{14}C yr BP frames. Pollen Viewer does not indicate any decreases in range or in magnitude of abundances for oak, birch, or sugar maple during that period. In fact, Pollen Viewer reflects an increase in the range of birch and increases in the general abundance of sugar maple pollen from 6,000 ^{14}C yr BP to 5,000 ^{14}C yr BP.

One could argue that increases in fire evidence occurring in association with the hemlock decline could be an indication of a warmer, drier climate more conducive to fire initiation and spread. Results for fuel loads and fire behavior from this study suggest that increased charcoal abundances probably reflect increased fire activity. Furthermore, charcoal increases seen at these five sites are all short-lived; there are no sustained increases in charcoal levels. If the short-lived fire increases seen in the data were related to climate-driven changes in fire regimes, they could only be due to short-lived pulses of warmer, drier weather. Since hemlock required 1,000 to 2,000 years to recover, short-lived climate changes are not supported. Furthermore, when charcoal increases in association with the hemlock decline it most often does so during or after the decline, not before which one might expect if climate alone were causing increased fire activity.

Overall, my data do not support the climate-driven hemlock decline hypothesis. Neither oak nor northern hardwoods decline contemporaneously with the major hemlock decline, and increased fuel loads from dead hemlock provide a feasible explanation of increased fire activity independent of sustained drier climate. Based upon my analysis, a biological agent seems the more probable proximate cause of the decline, although the debate regarding the cause (or causes) will likely continue for some time.

Conclusions

An apocryphal tale of science has Galileo scaling the steps of the Leaning Tower of Pisa from where he dropped two cannonballs of different sizes but the same material. The balls hit the ground at the same time, proving that acceleration due to gravity is constant irregardless of mass and shattering the Aristotelian view that gravitational acceleration would cause heavy objects to fall faster than light objects. It would be a gratifying universe indeed if all scientific research provided such clear and simple answers. Unfortunately, most scientific research, especially in highly complex ecological systems, does not yield simple answers but complicated or even obscure ones and often generate more questions than they answer. This is the way in which science progresses. Galileo's question was "is the acceleration due to gravity constant?" The answer was "yes". The primary question of this project was "did fire activity increase after the hemlock decline?" The answer is "well, it depends." The conclusions are best addressed by considering the original postulates formulated in the introduction.



The first postulate is that hemlock mortality produces heavy loadings of available fuels in areas where available fuel loadings are normally low (or perhaps moderate in old growth stands). This is true, as demonstrated by the fuels study in which both fuel loadings and predicted fire behavior are greatly increased in adelgid-killed stands of hemlock. There is a lack, however, of even anecdotal evidence that adelgid-affected stands are experiencing increased fire (or any fire at all). Modern hemlock stands are generally restricted to cool, moist habitats where fires are less likely. There is an abundant ignition source (people), but the public is strongly cautioned to avoid starting wildland fires. Add to this vigorous and effective fire detection and suppression, and significant barriers to the spread of fire (roads, agricultural fields, *etc*.), and it is understandable that fires are not frequently found in hemlock stands. Also consider that the weather and topography constants used in the fuel models were realistic but moderately severe and not commonly encountered. In the mid-Holocene, there was no fire suppression and fewer barriers to the spread of fire, so low-intensity fires could have spread into dead hemlock stands and intensified. Also, hemlock occurred more widely on the landscape and presumably was not as restricted to cool, moist sites as it is today.

The second postulate is that frequent high intensity fires outside of the "normal" fire regime occurred following the decline of hemlock. This postulate is clearly true for some sites but not others. At three sites (The Bowl, Lake Wood, and Round Pond) increased fire activity is closely associated with the hemlock decline, but at Hawley Bog and Larkum Pond there is no clear link. Charcoal peaks at the first three sites occur shortly after the onset or during the major hemlock decline, and then return quickly (within six or so samples, *i.e.*, 100-200 years) to low background levels. This directly supports postulate three: that fire increases were short-lived, persisting only until increased fuels were consumed. The Bowl and Lake Wood are coastal sites (both are on Mount Desert Island, Maine) and Round Pond is close to the Connecticut River at the edge of a fire-prone outwash plain (Westfield, Massachusetts). Larkum Pond and Hawley Bog are high elevation inland sites. Patterson and Sassaman (1988) argue that for New England, prehistoric fire ignitions were most common in coastal areas and along major rivers, because aboriginal populations (the primary ignition source) were higher there. Additionally, sites which are dry due to very well-drained soils, such as around Round Pond, would be more fire-prone than mesic sites. These facts coupled with the pollen data of this study lead to the conclusion that increases in fire may have occurred following the hemlock decline, but fire regimes were moderated by the inherent flammability of the environment. This conclusion supports the fourth postulate that within New England, fire regime changes were greatest where fire potential was greatest.

The fifth postulate - that hemlock was quickly replaced by pioneering tree species and then succeeded to northern hardwood-dominated stands - is supported in part by the results. All five sites experienced at least a brief increase in birch pollen, three species of which are early successional, during the later stages of the decline. Pollen from The Bowl, Lake Wood, and Hawley Bog demonstrate a sustained increase in beech, considered a component of northern hardwood forests, following the decline. Sugar maple, another northern hardwood species, has a slight but sustained increase at Hawley Bog after the decline and a surge during the decline at Round Pond, but remains more or less stable at the other sites. In contrast, Larkum Pond has a steady, sustained increase in oak after the decline, whereas Round Pond has a decrease in oak and sustained increases in pine and birch. It seems that the types of late-successional species that come to dominate a site following the decline are not necessarily northern hardwoods, but depend upon the climate, soils, and disturbance regime, and perhaps most importantly, seed sources.

In summary, the results of this study indicate the fire was not universally a significant factor driving post-hemlock-decline succession. The degree to which fire influenced post-decline vegetation is based largely on the degree to which fire occurred on the landscape before the decline.

Further research

More sites should be subject to paleoecological study by re-analyzing existing data (from the National Surface and Fossil Pollen Database, for example), re-examining existing materials (*i.e.*, from previously recovered sediment cores), or retrieving new sediment cores from previously unstudied sites. Highest priority should be given to sites where hemlock was dominant on the landscape before the decline and the fire regime was active. Such sites may be difficult to find as hemlock is not generally common in fire-prone environments. Possibly, sites along the Maine coast (similar to The Bowl and Lake Wood), around Lake Ontario, or in the mid- to southern Appalachians would provide the requisite combination of abundant hemlock and fire. Examination of existing data would be most efficient, but most paleoecological studies do not quantify the abundance of charcoal. Re-analysis of material from existing cores would be the next most expedient option as one could choose cores in which hemlock pollen is known to be abundant before the major decline based on the initial analysis of the core. Extracting new sediment cores would be the most laborious option, but also most likely to be most fruitful. Such replication would help to refine and strengthen or perhaps redirect the conclusions of this study.

Obtaining absolute values for pollen at the five study sites would help strengthen or redirect conclusions of this study by potentially eliminating much ambiguity in the results, particularly in regards to the relative abundance issues of percentage data. Reliable pre-decline and post-decline dates would have to be obtained to facilitate accurate pollen influx calculations. Because of the small amount of sediment at each depth available for analysis, Accelerator Mass Spectrometry ^{14}C radiocarbon dating is necessary for accurate dating of sediments. At around $600 per sample at the time of this writing, full analysis of all five sites would cost approximately $6000. The sediments from The Bowl and Lake Wood are no longer available. In addition to the cost of radiocarbon dating, therefore, one must add the cost and effort to recover new sediment cores from each of those sites and conduct enough pollen analysis to clearly determine the depth of the major hemlock decline in the sediments. Thus, obtaining absolute pollen values for all five sites is probably prohibitively expensive.

Since birch pollen was not identified to species at the level of analysis conducted here, identifying which birch species were present just before, during, and soon after the decline would help confirm or redirect conclusions. Early successional birch species were assumed to contribute to the rise in birch pollen following the major hemlock decline, but which species (*B. papyrifera, B. populifolia,* or *B. lenta*) and was it the same species at all sites? Macrofossil analysis, specifically the identification of fossil birch seeds in the sediments to the species level, might be informative in this regard. Re-analysis of existing material from Hawley Bog, Larkum Pond, and Round Pond with attention to differentiating gray birch pollen to the species level is another possibility, however, it is more likely that black birch is the species that is responding (which cannot be differentiated by pollen).

Finally, continuous sampling of Larkum Pond sediment levels spanning the hemlock decline would be desirable to assure no very short-lived peaks in charcoal were missed. Recall that Hawley Bog and Round Pond were sampled continuously (1 cm thick samples taken every centimeter) around the time of the decline. Larkum Pond has a much higher sedimentation rate, so the sediment was sampled every 3 cm to 5 cm to provide a similar temporal resolution. If the heavy fuel loads of dead hemlock burned in a single fire in the Larkum Pond region, the resulting charcoal peak might be missed without continuous sampling.

APPENDIX

TAXA NAMES

Common names of species and other taxa are used in this document with the scientific name provided parenthetically at first mention. Common and scientific names also are presented here for reader convenience.

common name	scientific name
alder	*Alnus* spp.
American chestnut	*Castanea dentata*
aspen/cottonwood	*Populus* spp.
Atlantic white cedar	*Chamaecyparis thyoides*
beech	*Fagus grandifolia*
black birch	*Betula lenta*
black cherry	*Prunus serotina*
bracken	*Pteridium* spp.
buttonbush	*Cephalanthus occidentalis*
eastern hemlock	*Tsuga canadensis*
elongate hemlock scale	*Fiorinia externa*
elm	*Ulmus* spp.
grass	Family Poaceae
gray birch	*Betula populifolia*
hemlock borer	*Melanophila fulvoguttata*
hemlock looper	*Lambdina fiscellaria fiscellaria*
hickory	*Carya* spp.
northern red oak	*Quercus rubra*
pitch pine	*Pinus rigida*
red maple	*Acer rubrum*
red pine	*Pinus resinosa*
red spruce	*Picea rubens*
ruffed grouse	*Bonasa umbellus*
scarlet oak	*Quercus coccinea*
scrub oak	*Quercus ilicifolia*
spruces	*Picea* spp.
spruce budworm	*Choristoneura fumiferana*
sugar maple	*Acer saccharum*
swamp white oak	*Quercus bicolor*
sycamore	*Platanus occidentalis*
white ash	*Fraxinus americana*
white oak	*Quercus alba*
white pine	*Pinus strobus*
white-tailed deer	*Odocoileus virginianus*
wild turkey	*Meleagris gallopavo*

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